SERGIO ZUCATELI ALOQUIO JUNIOR

SISTEMÁTICA E FILOGENIA DE DIAPERINAE (COLEOPTERA: TENEBRIONIDAE)

Tese apresentada à Universidade Federal de Viçosa, como parte dos requisitos exigidos pelo Programa de Pós-Graduação em Ecologia para a obtenção do título de *Doctor Scientiae*.

Orientador: Cristiano Lopes Andrade

Coorientadores: Lucimar Soares de Araujo
Paschoal Coelho Grossi

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“Tali [facili da intendersi] sono tutti le cose vere, doppo che sono trovete; ma il punto sta nel saperte trovare.”

Galileo Galilei

“I am turned into a sort of machine for observing facts and grinding out conclusions.”

Charles Darwin

RESUMO

ALOQUIO JUNIOR, Sergio Zucateli, D.Sc., Universidade Federal de Viçosa, fevereiro de 2020. **Sistemática e Filogenia de Diaperinae (Coleoptera: Tenebrionidae)**. Orientador: Cristiano Lopes Andrade. Coorientadores: Lucimar Soares de Araujo e Paschoal Coelho Grossi.

Tenebrionidae é a sétima maior família de besouros, com cerca de 20.000 espécies descritas, classificadas em nove subfamílias. Uma dessas subfamílias, Diaperinae, é o objeto central dessa tese. Diaperinae é uma subfamília diversa em número de espécies, mais de 2.000, em hábitats, que abrangem desde basidiomes de fungos em florestas tropicais até dunas de areias nos litorais e ambientes xéricos. Essa diversidade de hábitats reflete na imensa diversidade morfológica dessa subfamília, e em grandes problemas de classificação dessa, que é a subfamília mais taxonomicamente problemática dentro de Tenebrionidae, perdendo somente para Tenebrioninae. O objetivo com esse trabalho está em buscar caracteres de importância taxonômica e filogenética, bem como resgatar uma hipótese de relações filogenéticas para Diaperinae. Almejando atingir esses objetivos, a presente tese foi dividida em quatro capítulos. No capítulo I, uma nova espécie de *Lelegeis* é descrita, com descrição detalhada de estruturas pouco usadas na taxonomia do grupo, tais como terminálias abdominais de macho e fêmea, bem como dados de sua biologia. No capítulo II, *Neanopidium mexicanum* é redescrito, adicionando detalhes da morfologia das terminálias de macho e fêmea, além de estruturas do aparelho bucal não mencionadas na descrição original. No capítulo III, foi realizado um estudo comparativo das terminálias de fêmeas de táxons supragenéricos de Diaperinae, listando 19 caracteres com possível sinal filogenético e descrevendo as terminálias abdominais de fêmeas para cada tribo de Diaperinae. No capítulo final, 29 espécies, incluindo grupos interno e externo, foram analisadas, gerando uma matriz com 123 caracteres morfológicos, dos quais 120 foram utilizados na análise filogenética que resultou em uma única árvore. Diaperinae apareceu como polifilético e Nilioninae, uma subfamília que já foi classificada como tribo de Diaperinae, apareceu como proximamente relacionada à Diaperini. Os detalhes das relações entre os táxons estudados são discutidos no capítulo.

Palavras-chave: Caracteres morfológicos. Morfologia comparada. Nova espécie.

ABSTRACT

ALOQUIO JUNIOR, Sergio Zucateli, D.Sc., Universidade Federal de Viçosa, February, 2020. **Systematics and Phylogeny of Diaperinae (Coleoptera: Tenebrionidae)**. Adviser: Cristiano Lopes Andrade. Co-advisers: Lucimar Soares de Araujo and Paschoal Coelho Grossi.

Tenebrionidae is the seventh largest beetle family in number of species, with 20,000 described species classified into nine subfamilies. One of these subfamilies, Diaperinae, is the object of study for this thesis. Diaperinae is a quite diverse subfamily in number of species, with more than 2,000 species, in habitats, covering from fungi basidiomes to costal sand dunes and xeric environments. This habitat diversity reflects into the morphological diversity in the subfamily, and in many classification problems in this subfamily, that is one of the most taxonomically problematic subfamilies in Tenebrionidae, behind only the Tenebrioninae. The aim with this thesis is to find characters with taxonomic and phylogenetic importance, and to propose a phylogenetic hypothesis for Diaperinae. Looking for those goals, this thesis is divided into four chapters. In the chapter I, a new species of *Lelegeis* is described, with detailed description of the male and female abdominal terminalia, and notes on its biology. In the chapter II, *Neanopidium mexicanum* is redescribed, complementing with morphological characters not mentioned in the original description, such as the male and female abdominal terminalia and characters of the buccal apparatus. In the chapter III, a comparative morphological study of the female abdominal terminalia of the Diaperinae suprageneric taxa was conducted, resulting in a list of 19 characters with possible phylogenetic sign and the description of the female abdominal terminalia for each tribe. In the final chapter, 29 species, including ingroup and outgroup, were analyzed, returning 123 morphological characters of which 120 were used in the phylogenetic analysis, resulting in one single tree. Diaperinae appeared as polyphyletic and Nilioninae, once a tribe of Diaperinae, appeared close related to Diaperini. Details of the relations between the analyzed taxa are given in the chapter.

Keywords: Comparative morphology. Morphological characters. New species.

SUMÁRIO

INTRODUÇÃO GERAL

Tenebrionidae é a sétima maior família de besouros, com cerca de 20.000 espécies organizadas em 2.300 gêneros (Matthews *et al.* 2010, Ślipiński *et al.* 2011). A família apresenta distribuição mundial, com maior número de espécies nas regiões tropicais e temperadas, e fracamente representada acima do paralelo 50 N (Matthews *et al.* 2010). Tenebrionidae possui grande importância ecológica, participando da ciclagem de nutrientes em diversos ambientes, principalmente nas regiões áridas e semiáridas (Matthews & Bouchard 2008, Matthews et al. 2010). A adaptação à ambientes secos permite que esses besouros sobrevivam em condições onde a umidade é baixa, como em locais de armazenamento comercial de grãos (Calkins & Kirk 1975). Assim, muitas espécies possuem grande importância comercial e são consideradas pragas de grãos armazenados, como *Tribolium castaneum* (Herbst), *Gnatocerus cornutus* (Fabricius), *Alphitobius diaperinus* (Panzer), entretanto, por aparecerem em conjunto com besouros de outras famílias e em menor número, são considerados de menor importância e pouco se sabe sobre seu real impacto econômico (Watt 1974), exceto *Eleodes hispilabris* (Say, 1824), que foi mensurado como uma importante praga de trigo em Idaho, sendo responsável por perdas em torno de 10% da produção no início do século XX (Wakeland 1926). As larvas podem se alimentar de raízes em plantações comerciais, como espécies dos gêneros *Gonocephalum* Chevrolat e *Isopteron* Hope (Lawrence & Ślipiński 2013). O gênero *Tribolium* Macleay, em especial as espécies *T. castaneum* (Herbst, 1797) e *T. confusum* Jaqcquelin du Val, 1868, apresenta uma grande importância científica, tendo se tornado modelo para estudos de comportamento, ecologia e biologia de insetos, graças à facilidade de criação e ao seu rápido ciclo de vida (Watt 1974).

Atualmente, Tenebrionidae está dividida em 9 subfamílias, a saber: Alleculinae, Diaperinae, Lagriinae, Nilioninae, Phrenapatinae, Pimeliinae, Stenochiinae, Tenebrioninae, Zolodininae. À exceção de Nilioninae, com distribuição restrita à região Neotropical (sensu Morrone 2014), e Zolodininae, restrita à região Australiana, as subfamílias de Tenebrionidae apresentam distribuição cosmopolita (Matthews & Bouchard 2008). Cerca de metade da diversidade da família se encontra em Pimeliinae, uma subfamília com significativa representatividade em regiões áridas e semiáridas, por vezes perfazendo cerca de 80% de toda a diversidade nessas regiões, como é o caso do deserto da Namíbia (Lovegrove 1993).

Os hábitos alimentares de Tenebrionidae são dos mais variados, sendo o hábito predominante a eurifagia (Buxton 1924, Rogers et al. 1988), e acredita-se que o hábito ancestral seja a detritivoria e fungivoria, ainda muito frequentes dentro da família (Matthews & Bouchard 2008). Diaperinae é a subfamília focada na presente tese.

Histórico do estudo de Tenebrionidae no Brasil

Tenebrionidae é uma família historicamente negligenciada no Brasil, não havendo um especialista residente desenvolvendo trabalhos de taxonomia com essa família. Uma forte evidência para essa afirmação é o baixo número de espécies registradas para o Brasil, dada a sua grande extensão territorial e variedade de hábitats. São registradas cerca de 1300 espécies distribuídas em cerca de 60 gêneros (Spiessberger et al. 2020), sendo esses registros concentrados em áreas florestais, estando nosso Cerrado e Caatinga praticamente não representados (Aloquio 2016, Aloquio, Grossi & Lopes-Andrade 2019). Os primeiros registros e descrições de espécies para o território brasileiro datam do início do século XIX, sendo as primeiras espécies, à exceção das espécies introduzidas, descritas por Fabricius em 1801 (Spiessberger et al. 2020). A maior parte das espécies descritas para o território brasileiro datam do início e meados do século XX, sendo realizadas, em sua maioria, por Pic, Champion e Kulzer (Spiessberger et al. 2020).

Um importante trabalho para a fauna brasileira de Tenebrionidae foi a dissertação de mestrado da Maria Eulina Jorge (1974a), onde ela tratou das espécies de Nilioninae, na ocasião, ainda considerada uma família separada de Tenebrionidae. Esse trabalho resultou em descrições de larva (Jorge 1974b) e uma revisão, não publicada, das espécies da subfamília. Entretanto, não houve continuação nos trabalhos com Tenebrionidae, sendo a dissertação sua última contribuição para o grupo. Desde então, apenas outros dois brasileiros desenvolveram e desenvolvem trabalhos com Tenebrionidae, eu, Sergio Aloquio (Aloquio 2016, Aloquio & Lopes-Andrade 2015, 2016, 2017, 2019, Aloquio, Flores & Lopes-Andrade 2017, 2019, Aloquio, Grossi & Lopes-Andrade 2019) e Erich Spiessberger (Ivie & Spiessberger 2017, Spiessberger & Ivie 2018, Spiessberger & Mermudes 2018), atualmente doutorando da Univesity of Tüebingen, entretanto, esse último, desde o mestrado não desenvolve trabalhos com a fauna brasileira.

Estudos de morfologia comparada em Tenebrionidae

Alguns poucos estudos de morfologia comparada foram feitos para Tenebrionidae, em sua maioria realizados em meados de 1970 e 1980 (Doyen & Tschinkel 1982, Tschinkel 1975, Tschinkel & Doyen 1980). Trabalhos recentes de morfologia comparada focam em poucas espécies (Wagner & Gosik 2016) ou em uma tribo (Iwan 2001, 2002, 2004, Iwan & Kaminski 2016). Nenhum trabalho de morfologia comparada foi feito até o momento pra Diaperinae, contando com apenas algumas poucas espécies estudadas comparativamente (Doyen & Tschinkel 1982, Tschinkel & Doyen 1980).

Diversidade, distribuição e classificação de Diaperinae

Diaperinae possui pelo menos 2000 espécies viventes, classificadas em 118 gêneros e 11 tribos (Kergoat et al. 2014a), além do gênero *Triplehornia* Matthews & Lawrence, 2005, *incertae sedis* dentro da subfamília (Matthews & Lawrence 2005). Diaperinae é fracamente representado em registros fósseis, contendo 15 espécies descritas sendo o registro mais antigo encontrado no Paleoceno de Menat (França) datando de cerca de 61 – 56 milhões de anos (Nabozhenko 2019).

Diaperinae está distribuída por todo o globo, sendo mais diversa nas regiões florestadas dos trópicos (Matthews & Bouchard 2008). Algumas tribos possuem uma distribuição limitada, como é o caso de Ectychini, endêmica da Austrália, Hyociini, endêmica da região Australiana, Leiochrinini, encontrada nas regiões Oriental e Australiana, e também o gênero *incertae sedis Triplehornia*, encontrado em florestas úmidas das regiões Oriental e Australiana (Matthews & Bouchard 2008).

Diaperinae foi proposta como subfamília por Watt (1974), entretanto, desse trabalho, o único grupo que permanece na subfamília é a tribo Diaperini. As outras três tribos que o autor propôs como parte de Diaperinae, sendo elas Dysantini, Bolithophagini e Rhipidandrini, hoje estão dentro de Tenebrioninae, a primeira, sinonimizada com Toxicini, e as duas últimas unidas em Bolithophagini (Bouchard et al. 2005, 2011). A partir do trabalho de Bouchard e colaboradores (2005) a classificação de Diaperinae não sofre modificações, estando com as 11 tribos que a compõem desde então. Embora a classificação supragenérica de Diaperinae permaneça inalterada nos últimos 15 anos, as dúvidas quanto à validade dessa classificação ainda permanecem (Matthews & Bouchard 2008).

Biologia de Diaperinae

Diaperinae apresenta forte associação com fungos, principalmente os conhecidos popularmente como orelhas-de-pau (Keleinikova 1963; Watt 1974). Entretanto, existem algumas tribos especializadas em outras fontes de alimentos, como Crypticini, Hyociini e Trachysceliini, com hábitos xéricos, que se alimentam de qualquer matéria orgânica que possam encontrar (Matthews *et al.* 2010). As larvas de Diaperini se alimentam de orelhas-de-pau, assim como os adultos (Matthews & Bouchard 2008, Matthews et al. 2010), as de Leiochrinini e *Triplehornia* vivem expostas em troncos, se alimentando de lichens (Matthews & Bouchard 2008) e as larvas das tribos que vivem em dunas e no solo, quando conhecidas, são forrageadoras de solo, por vezes se enterrando (Matthews & Bouchard 2008).

Importância científica e econômica de Diaperinae

Há um crescente interesse no estudo de besouros tenebrionídeos com algum grau de associação com fungos, em especial com suas estruturas reprodutivas (basidiomas). Esse interesse advém da alta diversidade desses organismos, da sua importância no processo de degradação de fungos e por serem ótimos modelos para estudos em Ecologia e Evolução. Os insetos micetócolos (aqueles com algum grau de associação com fungos) são divididos em micetoxenos (visitantes ocasionais de basidiomas, que os utilizam geralmente como refúgios), micetófilos (utilizam basidiomas como abrigo, recurso ou local de forrageio em alguma fase do desenvolvimento) e micetobiontes (associação obrigatória em que tanto larvas como adultos dependem exclusivamente de basidiomas como alimento) (Lopes-Andrade 2007, Novák 2014). Os Diaperinae são majoritariamente micetobiontes e de extrema importância em processos de ciclagem de nutrientes em ecossistemas terrestres, pois consomem grande biomassa fúngica, alterando-a quimicamente e disponibilizando nutrientes para outros organismos da cadeia trófica. Sem os micetobiontes, muitos nutrientes concentrados nos basidiomas ficariam indisponíveis por vários anos (Graf-Peters *et al.* 2011).

Há também algumas espécies de importância econômica, pragas de grãos armazenados, como *Gnatocerus cornutus*, uma praga de grãos armazenados de relativa baixa relevância, *Cynaeus angustus* (LeConte, 1851), praga de milho armazenado e algodão na América do Norte (Matthews et al. 2010) e *Ulomoides dermestoides* (Fairmaire, 1893), praga de grãos armazenados introduzida da Ásia na América do Sul (Matthews et al. 2010).

Conhecimento sobre a evolução dos Diaperinae

As diversas mudanças na classificação, com a troca de tribos com outras subfamílias de Tenebrionidae e até mesmo outras famílias (Doyen 1974, 1984, Doyen & Lawrence 1979, Doyen & Tschinkel 1982, Doyen, Matthews & Lawrence 1990, Bouchard et al. 2005) evidenciam o pouco conhecimento evolutivo que se tem da subfamília. Diaperinae possui dois extremos em relação à sua morfologia, possuindo diferenças consideráveis entre as tribos que a compõem atualmente, devido à grande especialização de algumas dessas tribos para determinados hábitos de vida (Matthews & Bouchard 2008), e, dentro de uma mesma tribo, os gêneros e espécies são facilmente confundidos, devido à baixa diferenciação morfológica (Aloquio 2016). Essa característica torna o trabalho taxonômico e, principalmente, o trabalho de filogenia baseada em caracteres morfológicos, trabalhos extensos e, esse último, pouco ou nada convidativo.

Uma recente filogenia molecular (Kergoat *et al.* 2014b), a primeira realizada para Tenebrionidae com um número considerável de genes analisados, evidenciou a problemática na classificação em três grandes subfamílias de Tenebrionidae: Diaperinae, Tenebrioninae e Pimeliinae. Dentre essas, Diaperinae, objeto de estudo da presente tese, apresentou-se como polifilética, formada por cinco linhagens distintas (Kergoat *et al.* 2014b). Entretanto, os autores não utilizaram representantes de todos os táxons supragenéricos e alguns táxons neotropicais que podem estar estreitamente relacionados com a subfamília, como os Nilioninae, também não foram incluídos nas análises, o que torna essa análise, embora extremamente robusta, pouco informativa para acessar, de fato, a história evolutiva de Diaperinae e táxons correlatos.

OBJETIVOS DA TESE

O principal objetivo com a presente tese é acessar uma hipótese de relação filogenética entre os táxons supragenéricos de Diaperinae, fazendo o uso de caracteres morfológicos de adultos. Cada um dos capítulos que compõem a tese apresentam um objetivo específico que se somam ao objetivo principal. Os objetivos de cada capítulo são discriminados abaixo:

Capítulo I: O objetivo principal nesse capítulo é descrever uma nova espécie de *Lelegeis* Champion para a Mata Atlântica brasileira, focando na descrição de caracteres pouco utilizados na taxonomia do grupo, como as terminálias abdominais de macho e fêmea.

Capítulo II: Nesse capítulo o objetivo é redescrever a espécie mexicana *Neanopidium mexicanum* Dajoz, 1975, acrescentando dados de morfologia não apresentados na descrição original.

Capítulo III: O objetivo nesse capítulo foi realizar um estudo de morfologia comparada das terminálias abdominais de fêmeas de Diaperinae, buscando por caracteres com possível sinal filogenético.

Capitulo IV: Aqui o objetivo foi apresentar uma lista de caracteres com sinal filogenético, buscando utilizar aqueles que são pouco usuais tanto em análises filogenéticas quanto na taxonomia, mas que enxergamos diferenças na comparação das espécies utilizadas.

ORGANIZAÇÃO DA TESE

Os resultados da presente tese são apresentados em quatro capítulos, a saber:

Capítulo I: A espécie *Lelegeis pitanga* **sp.nov.** é descrita, atentando para a descrição de caracteres negligenciados na taxonomia do grupo, mas que já vimos serem importantes na separação de táxons similares, como as terminálias abdominais de macho e fêmea. Atentamos também à importância de descrições completas para uma melhor compreensão da classificação do grupo, incluindo dados de biologia da espécie tratada. Esse capítulo está publicado na revista Zoologia: An International Journal for Zoology.

Capítulo II: *Neanopidium mexicanum* Dajoz, 1975 é redescrito nesse capítulo, tendo sua descrição complementada com informações de terminálias abdominais de macho e fêmea, bem como a descrição das setas encontradas no aparelho bucal, que apresentam características únicas à essa espécie, mas que não foram apresentadas na descrição original. Esse capítulo está publicado na revista Iheringia: Série Zoologia.

Capítulo III: Nesse capítulo, foi realizado um estudo de morfologia comparada da terminalia abdominal de fêmea para os táxons supragenéricos de Diaperinae. Foi escolhida a terminalia abdominal de fêmea, pois em trabalhos anteriores já havíamos observado sua importância taxonômica e possivelmente filogenética. Foram caracterizadas as terminálias de fêmeas para cada táxon supragenérico estudado e uma lista de 19 caracteres com possível sinal filogenético foram apresentados. Esse capítulo foi apresentado perante uma banca para a obtenção da qualificação no processo de doutoramento e, no momento, encontra-se em fase de revisão para a submissão na revista Zoologischer Anzeinger.

Capítulo IV: Nesse capítulo, foi realizado um estudo comparativo entre diversas espécies compreendendo todas as 11 tribos de Diaperinae e o gênero *incertae sedis Triplehorn*. Dessas, 15 foram selecionadas para compor o capítulo. Além dessas 15 espécies, outras 14 foram selecionadas, representando Ciidae e as outras subfamílias de Tenebrionidae, exceto Zolodininae. O estudo morfológico retornou 123 caracteres, dos quais 120 foram informativos e, portanto, utilizados na análise. Esse capítulo nunca foi apresentado à nenhuma banca e nem submetido para nenhuma revista.

CAPÍTULO I – A new species of *Lelegeis* (Coleoptera: Tenebrionidae: Diaperini) from the Atlantic Forest of Brazil

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RESEARCH ARTICLE

A new species of *Lelegeis* (Coleoptera: Tenebrionidae: Diaperini) from the Atlantic Forest of Brazil

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http://zoobank.org/D49B896E-ABE8-4463-8E03-E7238595550C

ABSTRACT. *Lelegeis* Champion, 1886 occurs only in the Neotropical region and comprises four species: *L. aeneipennis* Champion, 1886 from Mexico; *L. apicalis* Laporte & Brullé, 1831 from Cuba; *L. hispaniolae* Triplehorn, 1962 from Haiti and the Dominican Republic; and *L. nigrifrons* (Chevrolat, 1878) occurring in Brazil, Mexico, Panama, Peru and Venezuela. Here, *Lelegeis pytanga* **sp. nov.** is described based on specimens collected in the Atlantic Forest of Brazil, and the first detailed description of the sclerites of the male and female terminalia of *Lelegeis* is produced. The new species can be easily distinguished from the other *Lelegeis* by its dull reddish brown to reddish orange elytral coloration, while the remaining body surface is dull black. The morphology of *Lelegeis* and its generic boundaries within Diaperinae are discussed.

KEY WORDS. Darkling beetle, Diaperinae, host fungi, Southeast Brazil.

INTRODUCTION

Lelegeis Champion, 1886 was proposed by Champion (1886) for a single species, *L. aeneipennis* Champion, 1886, described from a single specimen from Cordoba, Mexico. Later, *Platydema apicalis* Laporte & Brullé, 1831, known only from Cuba, was transferred to *Lelegeis*, and *L. hispaniolae* Triplehorn 1962 was described from Haiti (type locality Ennery) and the Dominican Republic. *Platydema nigrifrons* Chevrolat, 1878, a very common beetle from Brazil (type locality Ega, nowadays Tefé, in the state of Pará), Mexico, Panama, Peru and Venezuela, was also transferred to *Lelegeis* (Triplehorn 2009). No subsequent work mentioned the genus.

The main and probably only feature that allows the separation of *Lelegeis* from the morphologically similar genus *Platydema* Laporte & Brullé, 1831 is the abnormally large and flattened basal protarsomere of the males (Triplehorn 1962). The current delimitation of *Platydema* is problematic, as the delimitation of other Diaperini genera such as *Cosmonota* Blanchard, 1846, which does not have any precise feature to distinguish it from *Platydema*; and *Liodema* Horn, 1870, with its peculiar anterior prolongation of the mesoventrite (Triplehorn 1962). Here, we describe *Lelegeis pytanga* sp. nov. from the Atlantic Forest of Brazil, and discuss the morphology of *Lelegeis* and the generic limits within Diaperini.

MATERIAL AND METHODS

About two thirds of the individuals of *Lelegeis pytanga* sp. nov. were collected between 2014 and 2017 at “Mata da Biologia”, “Mata do Paraíso” and “Parque Nacional do Caparaó”, which are remnants of the Atlantic Forest biome in Southeast Brazil. Additional individuals found in the collection of Instituto Oswaldo Cruz were collected in the Atlantic Forest of the state of Rio de Janeiro. Host fungi of the individuals collected by us were identified to species whenever possible.

Examination and dissection of adults were conducted under a Zeiss Stemi 2000-C stereomicroscope. Sclerites of the female terminalia, including the spermatheca, were stained with a solution of 0.5% Chlorazol Black E in 85% alcohol to enhance contrast. Whole mount preparations of dissected sclerites were made using a water-soluble mounting media based on polyvinyl alcohol and lactic acid. Slides were photographed under a Zeiss AxioLab compound microscope equipped with a Zeiss AxioCam

MRc. Adults were photographed under a Zeiss Discovery V20 stereomicroscope with a Zeiss AxioCam 506, and final images were the result of montaging 25 to 40 image slices at different focal lengths using the extended focus module of Zeiss ZEN 2012 software.

The description of *L. pytanga* sp. nov. was based mostly on the male holotype, except for the description of the female terminalia, which was based on a paratype. The terms for the external morphology, including sclerites of the abdominal terminalia, follow Matthews et al. (2010). The term "compound sensoria" as used here refers to the aggregation of sensilla, forming distinct multi-pronged structures (Medvedev 1977, Matthews et al. 2010). The following acronyms of measurements (in mm) and ratios are used throughout the text: EL, elytral length (at midline, from base of scutellar shield to elytral apex); EW, greatest elytral width; GD, greatest depth of the body (from elytra to metaventrite); PL, pronotal length along midline; PW, greatest pronotal width; TL, total length (= EL+PL; head not included). The ratio GD/EW was recorded as an indication of the degree of convexity; TL/EW indicates the degree of body elongation.

The labels were printed in white paper, unless otherwise specified. Label data are cited verbatim in quotation marks; a column separates each line of a label and a backslash separates different labels of a specimen. Square brackets are used to denote our comments on label data. The number, gender and depository of specimens bearing these labels are stated immediately before the label data.

Acronyms of depositories. (AMBC) Ayr Bello private collection, Rio de Janeiro, RJ, Brazil (Ayr de Moura Bello); (CEIOC) Coleção Entomológica do Instituto Oswaldo Cruz, FIOCRUZ, Rio de Janeiro, RJ, Brazil (Jane Costa); (CELC) Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera, Viçosa, MG, Brazil (Cristiano Lopes-Andrade); (CEMT) Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal do Mato Grosso, Cuiabá, MT, Brazil (Fernando Z. Vaz-de-Mello); (CERPE) Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, PE, Brazil (Paschoal C. Grossi)

TAXONOMY

Lelegeis pytanga sp. nov.

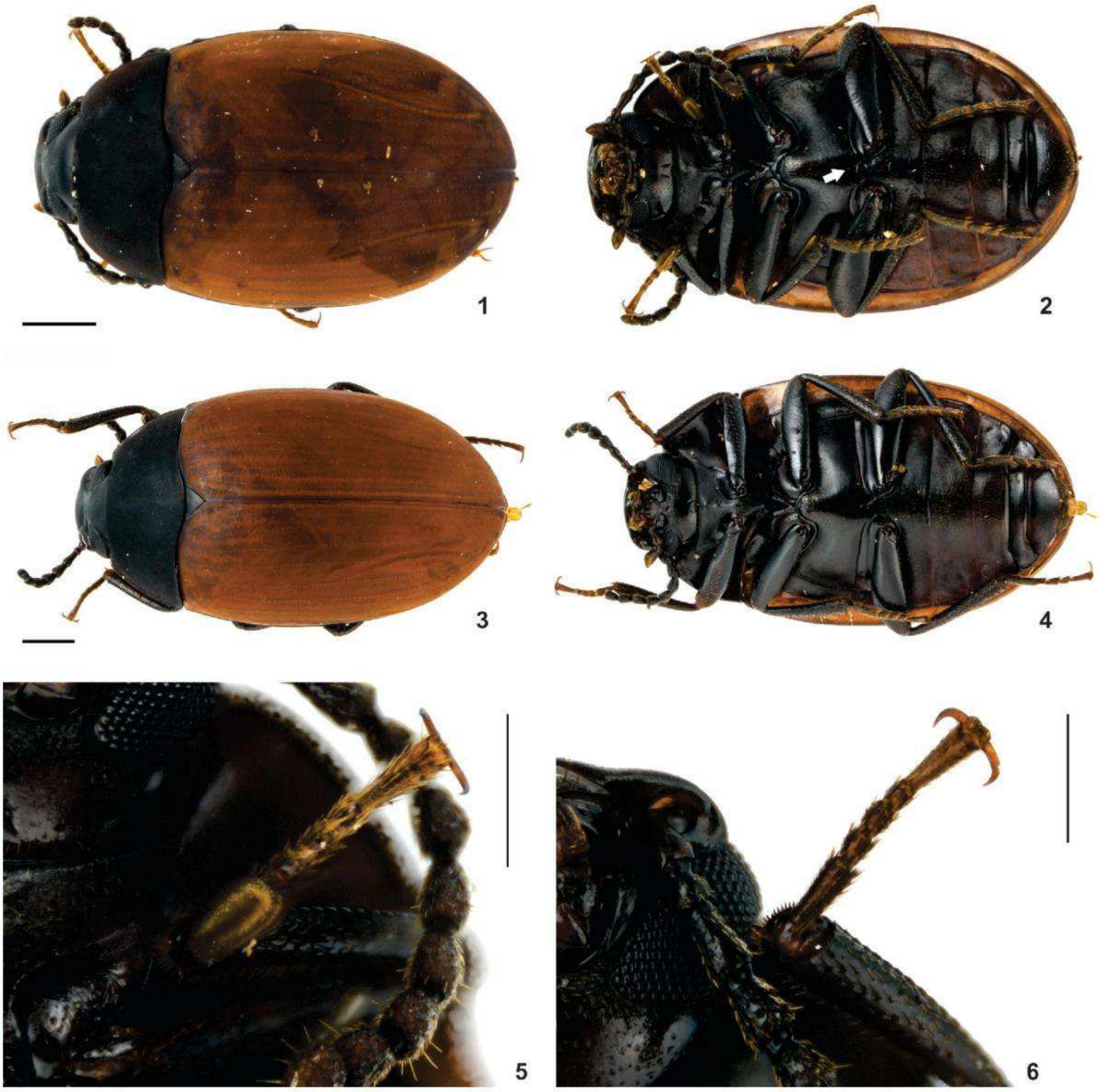
http://zoobank.org/74420FC0-7AA0-478A-B1D3-BDCE5866DF59

Figs 1–10

Type locality. Estação de Pesquisa, Treinamento e Educação Ambiental Mata do Paraíso (EPTEA Mata do Paraíso), Viçosa, state of Minas Gerais, Brazil, 20°48'08"S, 42°51'30"W.

Diagnosis. *Lelegeis pytanga* sp. nov. can be easily distinguished from the other species of the genus by its dull reddish brown to reddish orange elytral coloration, while the remaining body surface is dull black. *Lelegeis nigrifons* is light colored with dark spots, *L. hispaniolae* is entirely shiny dark reddish brown, *L. apicalis* is shiny dark brown and *L. aeneipennis* is shiny testaceous.

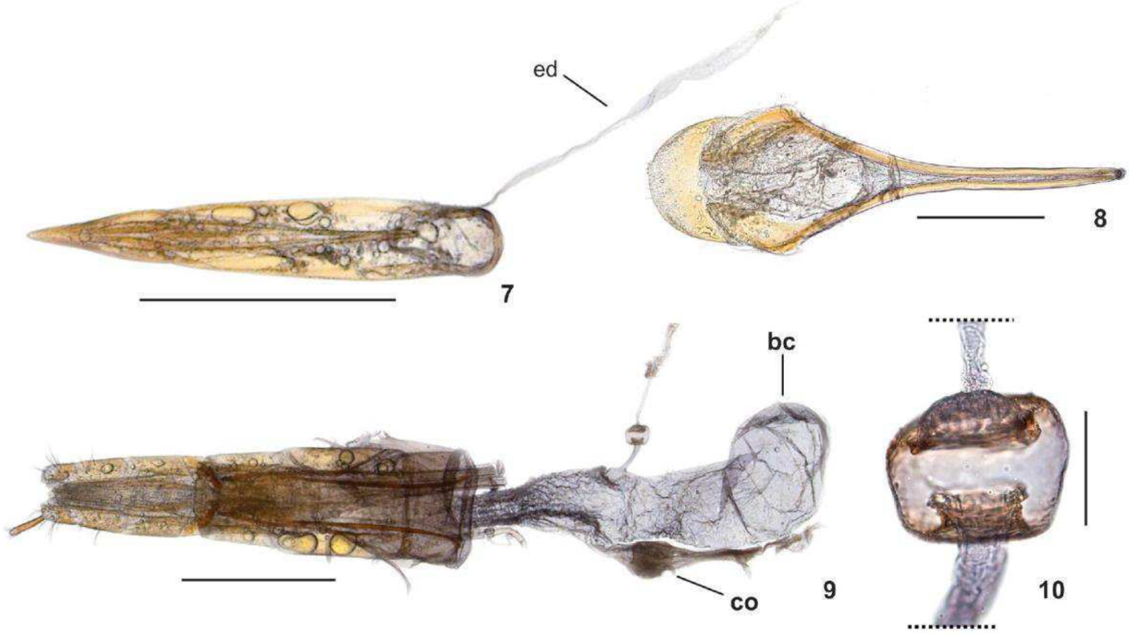
Description. Male, holotype (Figs 1–2, 5, 7–8). **Body** moderately convex, dull, glabrous; length 6.48 mm, width 4.00 mm; pronotum, head, scutellar shield, antennae and legs black, elytra reddish brown. **Head** finely punctate, rounded anteriorly; clypeus transverse, clearly defined, its punctation denser than that of the remaining head dorsum; epicanthus expanded and covering antennal insertions dorsally. **Eyes** with anterior portion emarginated by epicanthus, forming a lower lobe about 2.5 times as large as upper lobe. **Antennae** 11-segmented; antennomere 2 shorter than the remaining, about half the length of the antennomere 3; antennomeres 4–11 gradually expanded into a long, loose club, compound sensoria small, each with about the diameter of an ommatidium, distributed all over the surface of all the club antennomeres. **Pronotum** strongly transverse, trapezoidal, about 2.5 times as wide as long, widest at base; lateral edges explanate, visible for their entire lengths from above; anterior edge truncate and posterior edge sinuate; punctation not discernible. **Elytra** approximately 3.5 times as long as pronotum, widest at middle; epipleuron reaching elytral apex; punctation striate, with 8 striae on each elytron. **Hind wings** developed, apparently functional. **Ventral surface** shiny, with small golden setae; prosternal process rhombus-shaped, expanding to middle and then narrowing to apex. **Protibiae** with inner edge serrate; apex bearing a row of small spines; inner apical angle with two long, thick spines. **Tarsomeres** bearing two rows of small setae ventrally. **Protarsi** with the first protarsomere expanded (Fig. 5), about twice as wide as the others and about as long as the following three; basal protarsomeres with a ventral plaque instead of rows of setae. **Abdominal process** sharply acute. **Metaventrite** with a small median groove in the point of contact with the abdominal process (Fig. 2, arrow). **Aedeagus** (Fig. 7) dorso-ventrally flat; basale about 2.5 times as long as apicale; apicale widest at base, strongly narrowed from middle to apex, apex sharply acute; basale widest at basal 1/3, slightly curved ventrally; penis narrow, about as long as basale, membranous, except for the lateral edges. **Spiculum gastrale** (Fig. 8) Y-shaped, with posterior branches expanded. **Female paratypes** (Figs 3–4, 6, 9–10) similar to males except for the following features: **Protarsi** without modified basal tarsomere (Fig. 6). **Female abdominal terminalia** (Fig. 9) with bursa copulatrix about three times as long as gonocoxites together; bursa without window or other visible sclerites; common oviduct about as long as bursa; spermatheca(Fig. 10) about as long as the apical gonocoxite, devoid of check valve, with basal and apical cylindrical sclerotized invaginations, the basal invagination reaching about the middle of spermatheca, the apical invagination reaching about the apical 1/3 of the spermatheca and forming a dome-like structure apically; each side of ovipositor transversely divided into four gonocoxites; gonocoxites varying in length, with the basal gonocoxites small, bearing oblique baculi; second and third gonocoxites similar in length, about



Figures 1–6. *Lelegeis pytanga* sp. nov.: male holotype, habitus dorsal (1) and ventral (2) views. Female paratype, habitus dorsal (3) and ventral (4) views. Protarsomeres male (5) and female (6). Scale bars: 1–4 = 1 mm, 5–6 = 0.5 mm.

twice as long as the basal ones; each apical gonocoxite small, about as long as the basal, bearing long setae and one long gonostylus; gonostyli inserted almost laterally, about as long as apical gonocoxites, slightly expanding to apex, apex bearing five long setae; paraprocts about as long as gonocoxites together, bearing long parallel baculi. Proctiger long, slender, medially membranous, bearing baculi laterally.

Measurements. Male holotype (in mm). TL = 6.48, PL = 1.36, PW = 3.44, EL = 5.20, EW = 4.00, GD = 2.64; ratios: GD/EW = 0.66, TL/EW = 1.62. Male paratypes (in mm; n = 7). TL = 6.32–8.00 (7.19 ± 0.58), PL = 1.28–1.76 (1.52 ± 0.18), PW = 3.28–4.16 (3.73 ± 0.33), EL = 5.04–6.40 (5.67 ± 0.44), EW = 4.00–5.04 (4.54 ± 0.32), GD = 2.56–3.12 (2.85 ± 0.17); ratios: GD/EW = 0.59–0.68 (0.63 ± 0.03), TL/EW = 1.54–1.62 (1.58 ±



Figures 7–10. *Lelegeis pytanga* sp. nov.: (7) ventral view of aedeagus; (8) spiculum gastrale; (9) female terminalia; (10) spermatheca. (bc) Bursa copulatrix, (co) common oviduct, (ed) ejaculatory duct. Scale bars: 7–9 = 1 mm, 8 = 0.5 mm, 10 = 0.1 mm.

0.02). Female paratypes (in mm; n = 11). TL = 6.56–7.60 (7.27 ± 0.43), PL = 1.28–1.76 (1.60 ± 0.15), PW = 3.36–4.00 (3.76 ± 0.26), EL = 4.96–6.00 (5.66 ± 0.34), EW = 4.08–5.20 (4.67 ± 0.41), GD = 2.72–3.12 (2.93 ± 0.12); ratios: GD/EW = 0.55–0.73 (0.63 ± 0.06), TL/EW = 1.46–1.63 (1.56 ± 0.06).

Variation. Elytra varying in color from reddish brown to reddish orange.

Material examined. Holotype, male (CELC), labeled "BRASIL: MG, Viçosa; Mata do Para so; 11.x.2016; C. Lopes-Andrade & I. Souza-Gonçalves\ex *Hydnopolyporus fimbriatus*\HOLOTYPE *Lelegeis pytanga* Aloquio & Lopes-Andrade [red label]". Paratypes as follow: 1 female (CELC) labeled "BRASIL: MG, Viçosa; Mata do Para so; 11.x.2016; C. Lopes-Andrade & I. Souza-Gonçalves\ex *Hydnopolyporus fimbriatus*"; 1 male (CELC) labeled "BRASIL: MG, Viçosa; Mata do Para so; 17.v.2014; leg. C. Lopes-Andrade et al.\ex *Favolus tenuiculus*"; 1 male and 2 females (CELC) labeled "BRASIL: MG, Viçosa; Mata da Biologia, 18.ii.2015; leg. S. Aloquio, A. Orsetti & M. Bento; ex *Favolus tenuiculus*"; 1 male (CELC) labeled "BRASIL: MG, Viçosa; Mata do Para so; 03.ii.2014; LabCol leg."; 1 female (CELC) labeled "BRASIL: MG, Viçosa; Mata da Biologia; 26.x.2016; Orsetti & Pecci-Maddalena leg.\ex *Lentinus brumalis*"; 1 male (CELC) labeled "BRASIL: MG, Alto Capara ; PARNA do Capara ; Vale Verde 1200m; 06.xii.2016; Aloquio & Orsetti leg.\ex *Favolus tenuiculus*"; 3 females (1 AMBC, 1 CEMT and 1 CERPE) labeled "BRASIL: MG, Viçosa; EPTEA Mata do Para so; 14–15.xii.2016; 'trilha do pesquisador, perto das jabuticabeiras'; I. Pecci-Maddalena & C. Lopes-Andrade leg.\ex *Favolus tenuiculus*"; 1 female (CELC) labeled "BRASIL: MG, Viçosa; Mata da Biologia; 26.i.2017; Aloquio & Gomes leg.\ex *Favolus tenuiculus*"; 1 male (CEIOC) labeled "USINA TIJUCA; RIO DE JANEIRO; P BOHRNHEIM; 2/X/1963 [handwritten]\COLEÇ O FIOCRUZ"; 3 males and 3 females (CEIOC) labeled "Itatiaia; RJ – BRASIL; III-1933 [handwritten]; J. F. Zik n\Coleç o J F. Zikan". All paratypes are additionally labeled "PARATYPE *Lelegeis pytanga* Aloquio & Lopes-Andrade [yellow label]"

Host fungi. Specimens from Viçosa were collected once in *Hydnopolyporus fimbriatus* (Cooke) Reid (Meripilaceae) and *Lentinus brumalis* (Pers.) Zmitr. (Polyporaceae), and four times in *Favolus tenuiculus* P. Beauv. Larvae were not found and the number of individuals in each basidiome was low, thus these cannot be considered breeding records.

Etymology. The species name "*pytanga*" comes from the Tupi-Guarani, the most widely distributed indigenous language in Brazil, and means "red" or "reddish", in reference to the elytral color. The term "*pytanga*" is not Latinized and its ending is unchanged, so it does not agree in gender with the genus name.

Remarks. Triplehorn (1962) pointed out that another diagnostic feature for *Lelegeis* would be the mesotibiae of males being slender and straight for about half their lengths, then strongly curved and broadly expanded apically, being unmodified in females. However, we did not observe a significant difference between the mesotibiae of males and females, either in *L. pytanga* sp. nov. or *L. nigrifons*. Therefore, we did not add this character to the diagnosis of *Lelegeis*. The posterior median groove of the metaventrite, in contact with the abdominal process, is potentially a good feature for defining *Lelegeis*. However, its presence needs to be confirmed in species of *Lelegeis* that we have not examined (*L. aeneipennis*, *L. apicalis* and *L. hispaniolae*), and its absence in *Platydema* species needs to be confirmed. More accurate delimitations for Diaperinae genera may only be possible after a broad comparative morphological study of the character sets within the subfamily, especially characters that have been either completely neglected or insufficiently explored until now. A structure that can be easily examined, requiring only a small background in dissecting beetles, is the female abdominal terminalia. Our preliminary results show great differences in the morphology of the ovipositor, bursa copulatrix and spermatheca, all of which can be explored for taxonomic purposes. Differences in the sclerites of the female terminalia would be very helpful to separate females of *Lelegeis* from females of *Platydema*, which are almost identical in other characters.

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CAPÍTULO II – Complementary description of *Neanopidium mexicanum* (Coleoptera: Tenebrionidae: Diaperinae)

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Complementary description of *Neanopidium mexicanum* (Coleoptera: Tenebrionidae: Anopidiina)

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ABSTRACT. A complementary description for *Neanopidium mexicanum* Dajoz, 1975, type species of the genus, is provided based on specimens from the type locality Valle Nacional (Oaxaca, Mexico), including description and illustrations of male and female abdominal terminalia, which is provided for the first time to a *Neanopidium* species.

KEYWORDS. Abdominal terminalia, Diaperinae, Gnathidiini, Mexico.

Anopidiina is a poorly studied pantropical subtribe of Diaperinae comprising 13 genera and about 50 species (Doyen & Lawrence, 1979; Hopp & Ivie, 2008; Schawaller & Purchart, 2012). There were few works on Anopidiina in the last decade, with papers providing new distributional records (Hopp & Ivie, 2008), description of genus and species (Schawaller & Purchart, 2012) and solution to nomenclatural problem (Ivie & Spiessberger, 2017). *Neanopidium* Dajoz, 1975 is the most diverse genus of Anopidiina, considering extant species, with 13 described species known only from Neotropical areas of Mexico (Dajoz, 1975, 1977; Doyen & Lawrence, 1979). In the last four decades, there was no taxonomic work on the genus or further distributional data on its species.

A recent loan of unnamed specimens of Diaperinae from the Field Museum of Natural History (FMNH) revealed a small series recognized by us as *Neanopidium mexicanum* Dajoz, 1975. They are from the type locality, from the same field expedition in which the paratypes were collected, but possibly not examined by Dajoz. The original description is short and lacks information on important structures such as male and female abdominal terminalia. Our aim here is to provide a complementary description of *N. mexicanum*, with emphasis on structures not mentioned in its original description.

MATERIAL AND METHODS

Specimens were borrowed from the FMNH (Chicago, USA) as unidentified miscellanea of Diaperinae. The dissected specimens (one male, one female and one undetermined due to lack of abdomen) were immersed in hot water for a few minutes, and placed in a 20% KOH solution in an 80°C water bath for 10–20 minutes to soften and clarifying tissues. They were dissected under a Zeiss Discovery V8 stereomicroscope, and their mouthparts, antennae, metendosternite and abdominal terminalia were removed. The extracted female terminalia were stained in a solution of 0.5% Chlorazol Black E in 85% ethyl alcohol for enhancing contrast. Photographs of dissected mandibles were taken under a Zeiss AxioLab light microscope equipped with a Zeiss MRc digital camera; photographs of other dissected parts and habitus were taken under a Zeiss Discovery V20 stereomicroscope equipped with a Zeiss 506 digital camera. Measurements were made under a Zeiss Stemi 2000-C stereomicroscope with a scale ocular. Final images of the habitus were obtained merging photos of different focus using the software Helicon Focus 6 (licensed for the junior author).

Terms for external morphology, including sclerites of terminalia, follow Matthews *et al.* (2010). The following symbols are used for measurements (in mm) and ratios:

EL, elytral length (at midline, from base of scutellar shield to elytral apex); EW, greatest elytral width; GD, greatest depth of body (from elytra to metaventrite); PL, pronotal length along midline; PW, greatest pronotal width; TL, total length (head included); the ratio GD/EW was recorded as an indication of degree of convexity. Measurements provided here are only for the specimens examined by us. For a more complete range of variation in measurements and ratios, see the original description (DAJOZ, 1975).

TAXONOMY

Neanopidium mexicanum Dajoz, 1975

(Figs 1 – 12)

Material examined. Six specimens (one male, one female and four undetermined, FMNH), labeled: "MEX.: OAX.; 32mi S Valle Nacional, 7000' 22.v.1971 S. Peck Ber205, leaf litter".

Complementary description. Males with body (Figs 1-3) strongly convex, somewhat globose, shiny, glabrous except for labrum, legs, antennae and head; dorsum and venter dark reddish brown; mouthparts, legs and antennae dark golden yellow. Head coarsely punctate; punctures closest to each other in occipital region; clypeal suture barely discernible. Mandibles (Figs 4, 5) asymmetrical; outer edge with row of setae; mola and prostheca developed; prostheca membranous; bidentate. Maxillae (Fig. 6) with visible separation between galea and lacinia. Lacinia subcylindrical, with long, stiff setae apically. Galea trapezoidal, apex concave, with long, stiff setae. Maxillary palpi with four palpomeres; apical palpomere lanceolate; apex narrow, with small, rounded sensorial patch; area before apex with patch of small, spatulate sensillae (Fig. 7, arrow). Cardo semicircular. Mentum subquadrate. Labial palpi with three palpomeres; apical palpomere lanceolate, acute apex with rounded sensorial patch. Ligula pentagonal, with acute apex covered with short, stiff setae. Hypopharynx (Fig. 6) membranous, with a triangular sclerite (Fig. 6, arrow). Eyes absent. Antennae (Fig. 8) with 7 antennomeres (club counted as single antennomere, but seems to be fusion of three antennomeres with no visible suture between them, even in slide preparation); stellate sensoria (sensillifers; compound, multi-pronged sensoria *sensu* LAWRENCE *et al*., 2011) in inner and outer edges and apex of club; antennal insertions concealed in dorsal view by genal margins.

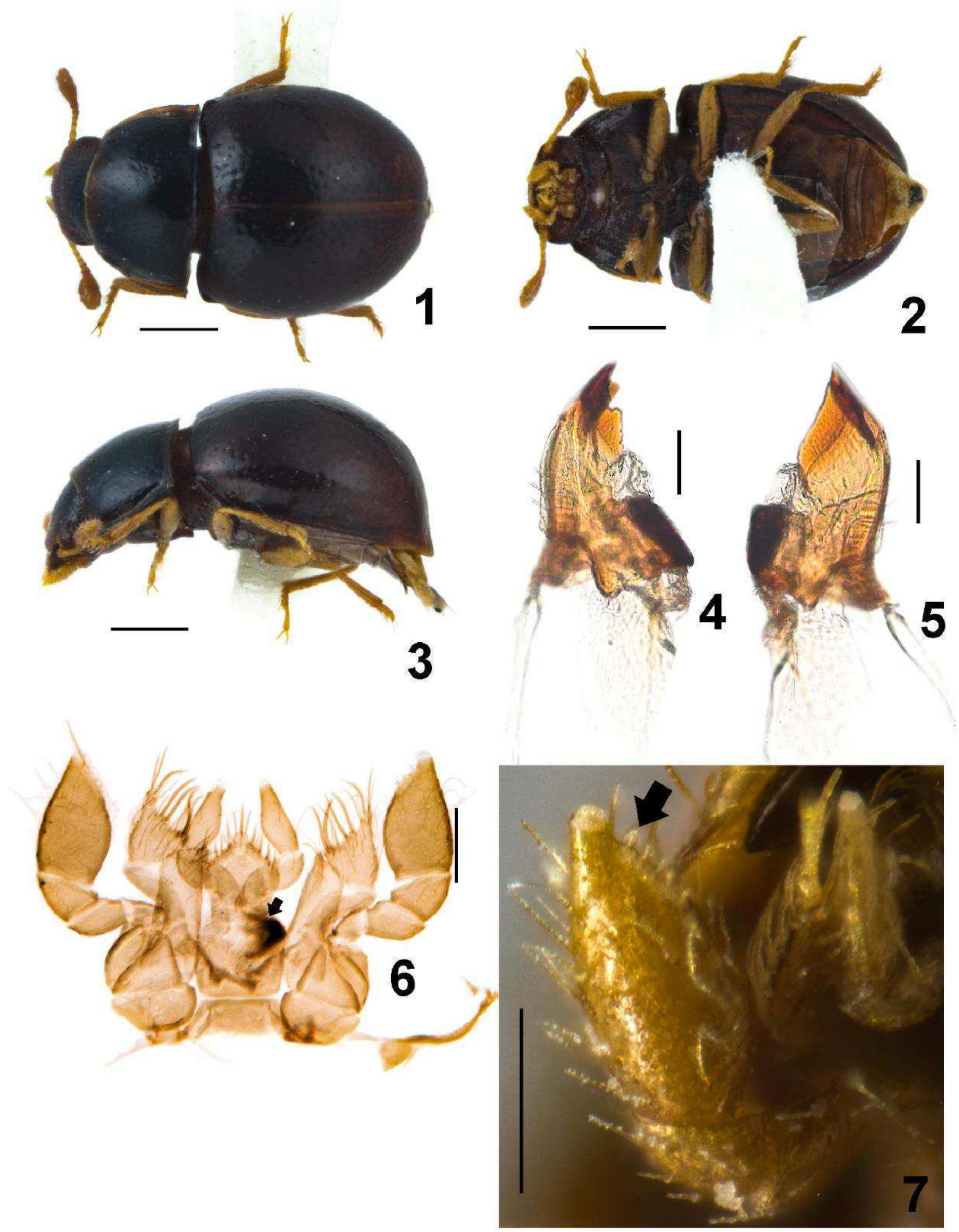
Pronotum finely punctate, comparatively finer than cephalic punctation; transverse, about 1.5x as wide as long, widest posteriorly and longest at middle; lateral edges explanate from anterior 1/3 to posterior edge; posterior angles acute; posterior portion not sinuous. Prosternal process large, about as wide as procoxa, subparallel-sided; apex truncate. Elytra about as long as wide in dorsal view, and about 1.8x as long as pronotum, wider at middle; epipleura with an indentation close to ventrite III, ending abruptly at beginning of last abdominal ventrite; punctation sparse, as coarse as on head. Metendosternite (Fig. 9) with short and narrow stalk, and long slender furcal arms; apex of furcal arms widened. Hind wings absent. Tibiae simple, pubescent, bearing row of spines apically, with two spines slightly longer in inner angle. Tarsal formula 4-4-4.

Abdomen with five ventrites; ventrites I–III connate, ventrites IV and V free; membrane visible between ventrites III–IV and IV–V; ventrites subparallel-sided until middle of ventrite III, than slightly enlarging to ventrite IV, narrowing to apex. Aedeagus (Fig. 10) with basale about 1.5x as long as apicale; apicale subtriangular, about twice as long as wide, widest at base; basale about 3x as long as wide, widest at middle, curved ventrally at basal 1/3; penis about as long as basale, lanceolate; ejaculatory duct about 2x as long as aedeagus. Spicullum gastrale (Fig. 11) horseshoe-shaped, enlarged at base of arms, each arm bearing one long seta basally.

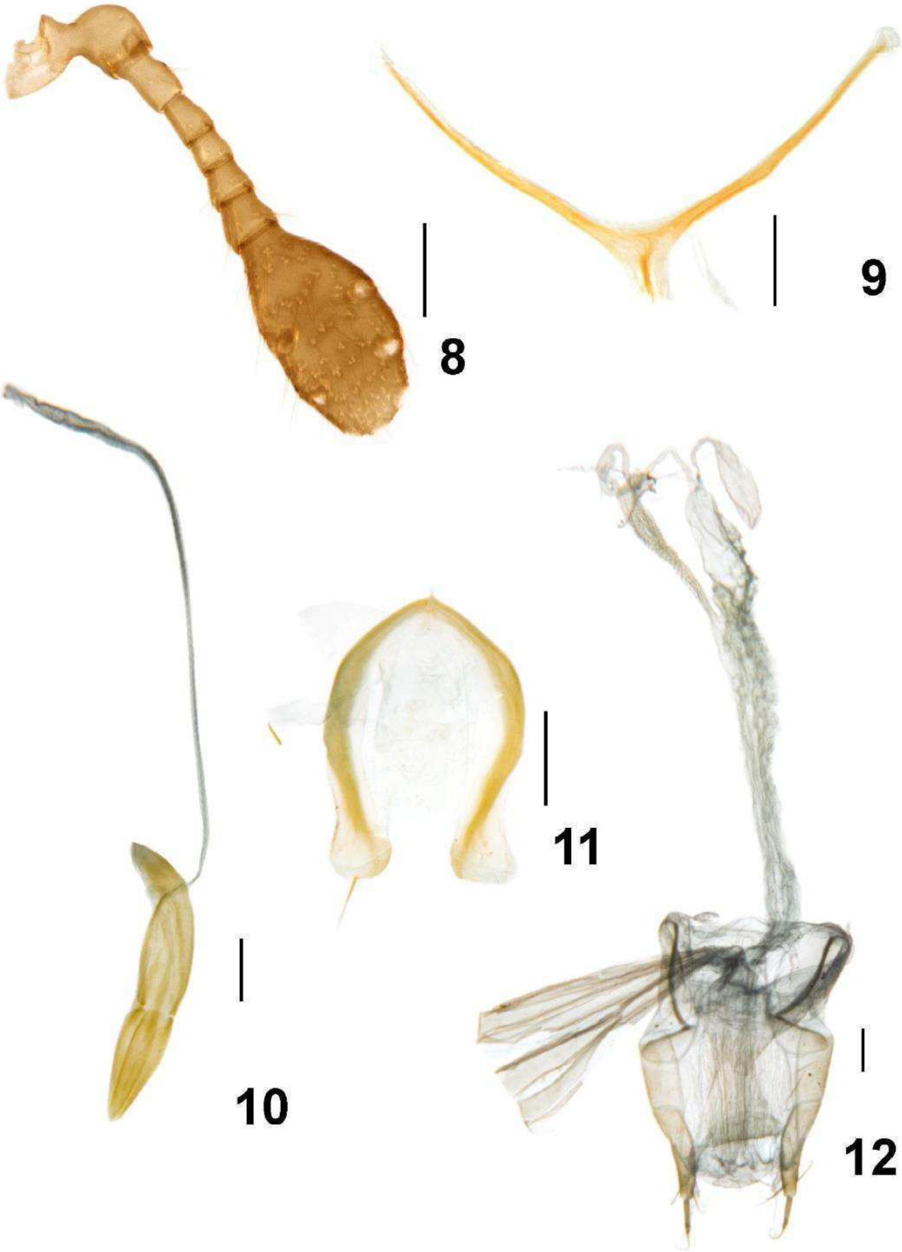
Females similar to males in exposed features. Terminalia (Fig. 12) with bursa copulatrix about as long as gonocoxites together; bursa copulatrix with apical balloon-shaped expansion, about as long as bursa; window of bursa and spermatheca absent; accessory gland tubular, about as long as gonocoxites together; ovipositor subquadrate, about as long as wide; paraprocts about 1/2 as long as gonocoxites together, bearing pair of baculi; baculi of gonocoxites oblique to baculi of paraprocts; gonocoxites ventrally divided into four lobes of subequal lengths; each apical lobe with long, slender gonostylus, surrounded by long setae; gonostyli as long as apical lobe of gonocoxites.

Variation. Measurements (in mm; n = 6): TL = 2.44–2.47 (2.46 ± 0.01), PL = 0.78–0.81 (0.79 ± 0.01), PW = 1.25–1.28 (1.26 ± 0.01), EL = 1.34–1.50 (1.41 ± 0.07), EW = 1.47–1.56 (1.50 ± 0.04), GD = 1.09–1.19 (1.14 ± 0.04). Ratios: GD/EW = 0.74–0.77 (0.76 ± 0.01), TL/EW = 1.58–1.68 (1.64 ± 0.04).

Comments. *Neanopidium mexicanum* differs from other species in the genus in being at least 2.4 mm long, with glabrous pronotum and elytra, elongate antennomeres I–IV, fine and sparse pronotal punctation that is comparatively finer than cephalic punctation, and lateral edges of pronotum not sinuous. The length range of *N. similis* and *N. pubescens* overlaps a little, but in the former the pronotal punctation is coarser than the cephalic punctation, and the lateral edges of pronotum are sinuous posteriorly. *Neanopidium pubescens* is conspicuously pubescent dorsally. The largest known *N. lawrencei* reaches 2.35 mm, very close to the smallest *N. mexicanum*, which are 2.4 mm long, but the former is easily discernable by its conspicuous dorsal pubescence. We failed to release specimens from the paper they were glued, even after using a modified Barber's fluid (formula of STÜBEN & LINSENMAIR, 2009). These specimens are from the same locality as the holotype and paratypes, collected only one day after some of the paratypes. It is important to note that the measurements of the studied series are within the variation mentioned in its original description, but with a comparatively smaller range, given the fewer specimens studied by us.



Figs 1-7. *Neanopidium mexicanum* Dajoz, 1975, habitus: 1, dorsal; 2, ventral; 3, lateral; mandibles: 4, left; 5, right; 6, labrum, maxillae and sclerite of hypopharynx (arrow); 7, detail of apical maxillary palpomere showing spatulate setae (arrow). Scale bars: 0.5 mm (Figs 1-3), 0.1 mm (Figs 4-7).



Figs 8-12. *Neanopidium mexicanum* Dajoz, 1975; 8, antenna; 9, metendosternite; 10, aedeagus in ventral view; 11, spicullum gastrale; 12, female abdominal terminalia. Scale bars: 0.1 mm.

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CAPÍTULO III – Comparative morphology of the female abdominal terminalia in Diaperinae (Coleoptera: Tenebrionidae)

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Comparative morphology of the female abdominal terminalia in Diaperinae (Coleoptera: Tenebrionidae)

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Abstract

Tenebrionidae is a large family of beetles, the seventh with more described species, comprising about 20,000 species in 9 subfamilies. Diaperinae is one of the most problematic subfamilies within Tenebrionidae, because its classification has been unstable in the last decades. The morphology of the female abdominal terminalia may provide informative taxonomical and phylogenetic characters that are neglected in Diaperinae. In the present study, we conduct a comparative study of the female abdominal terminalia, including the genital tract, ovipositor and related sclerites, between representative species of the 11 tribes of Diaperinae. We made comments regarding the most different morphologies, information available in the literature and our own observations on tenebrionid species. We also provide a list of characters with possible phylogenetic signal for Diaperinae.

Key-words: Abdominal sclerites; ovipositor; spermatheca.

Introduction

Tenebrionidae is the seventh family in number of species, with 20,000 species spread in 2,300 genera (Matthews et al. 2010, Ślipiński et al. 2011). Tenebrionidae is divided into nine subfamilies, Alleculinae, Diaperinae, Lagriinae, Nilioninae, Phrenapatinae, Pimeliinae, Stenochiinae, Tenebrioninae and Zolodininae, with only the last one not occurring in the Neotropics and Nilioninae being exclusive to that region (Matthews et al. 2010).

Diaperinae is a taxonomically problematic subfamily of the mega-diverse Tenebrionidae. Diaperinae can be found all around the world, but is most diverse in the tropics and comprises detritivorous species from a great range of habitats, from sand dunes to basidiomes of basidiomycetes fungi (Matthews et al. 2010).

Even though several researchers produced a great amount of works on Tenebrionidae in the last 60 years, the taxonomy of the family is still quite confusing, with the separation of genera resting in just a few characters, as well as the definition of tribes or even the subfamily. The phylogeny of the family based on molecular data (Kergoat et al. 2014) evidenced its classification problems, showing Diaperinae as polyphyletic, dismembered into five lineages, with Diaperini divided into two different clades.

No comparative study has been done, so far, in any aspect of morphology for the subfamily, and the female abdominal terminalia is neglected in almost all taxonomic works. Our aim here is to provide a comprehensive morphological study of the female abdominal terminalia of Diaperinae, address its importance to the taxonomy of this taxon and propose some characters that may be of phylogenetic importance.

Material and methods

For this comparative study, representatives of the 11 tribes of Diaperinae and the *incertae sedis* genus *Triplehornia* Matthews and Lawrence, 2005 were selected, following the currently accepted classification (Bouchard et al. 2011). The type genus and species of each tribe were included whenever available. For Diaperini, we included representatives of Adeliina and Diaperina.

The beetles were dissected under a Zeiss Discovery V8 stereomicroscope to extract the female abdominal terminalia and related sclerites. For minimize the risk of damaging the terminalia, the abdomen was extracted after submerging the whole beetle in hot water, and the abdomen were placed in a solution of concentrated KOH, and left overnight, to soften and clarify the membranes. The female abdominal terminalia were mounted in slides using a mounting media of polyvinylic acid, lactic acid and glycerin media. The contrast was enhanced by a stain solution of 5% Chlorazol Black E in 85% alcohol. The slides were photographed under a Zeiss Axiolab microscope equipped with a Zeiss Axiocam MRc scientific camera. The measurements were taken with the software ZEN 2012. Photographs of the habitus were made under a Zeiss Discovery V20 equipped with a Zeiss Axiocam 506 scientific camera with extended depth of focus, using 20–50 slices for composing the final image.

The morphological nomenclature follows Doyen and Tschinkel (1982) and Matthews et al. (2010). The list of characters follows the structure proposed by Sereno (2007).

The definitions of the morphological terms used in this paper are presented below, following the glossary of morphological terms (Lawrence et al. 2010) and the dictionary of entomology (Gordh and Headrick 2011):

Accessory gland. Gland associated with the spermatheca, usually either joined directly to it or to the spermathecal duct. Also known as spermathecal gland.

Baculum. Sclerotized bar or strut which serves to support a membranous ovipositor.

Bursa copulatrix. Enlargement of the female genital tract, which is often a blind sac at the anterior end of the tract (anterior bursa), but may be an enlargement section of the tract in the vicinity of the common oviduct (vaginal bursa).

Gonocoxite. One of two coxites associated with segment IX in female Coleoptera. Often divided into lobes ventrally.

Gonostylus. Small lobe articulated apically or sub-apically to the gonocoxite.

Ovipositor. The combined Proctiger, paraprocts, gonocoxites and gonostyli.

Paraprocts. One of two hemitergites or laterotergites of segment IX in most female beetles in which segment IX has become entirely divided into two parts which lie on either side of tergite X.

Proctiger. Tergite X in both male and female; lies immediately above the anal opening.

Spermatheca. Sac-like structure, often sclerotized; attached by a slender duct to the genital tract.

Spiculum ventrale. Anterior strut on sternite VIII in the female.

Vagina. Tubular structure formed by union of oviducts in female reproductive systems.

Vaginal sclerite. Hardened area found in the vagina.

Window of bursa. Framed portion of bursa copulatrix.

The studied beetles belong to the following collections (acronyms between parentheses): Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera (CELC), Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil; Australian National Insect Collection (ANIC), CSIRO, Canberra, Australia.

Results

Below we provide an overview of the female abdominal terminalia in Diaperinae and then descriptions of this structure for each examined species. Whenever necessary, comments are added to each description, mainly for providing additional information available in the literature or information on species examined by us but not included in the present work (for instance, when we have examined several species of a single genus). The taxa are organized by tribes, subtribes and then in alphabetical order.

General morphology of female abdominal terminalia in Diaperinae

Gonocoxites transverse to subquadrate, rarely long and slender, no more than 4 times as long as wide. Paraprocts from half to twice as long as gonocoxites. Gonocoxites without lobes to up to 4 lobes, usually with 4. Length of lobes variable, basal lobe usually shorter, not longer than 1/5 the length of ovipositor. Gonostyli present or absent; when present, length varying from 1/15 to 1/5 as long as ovipositor, inserted apically, laterally or, more rarely, dorso-laterally, apex usually bearing a long seta surrounded by small ones, usually 5. Paraprocts bearing baculi usually directed anteriorly, rarely laterally. Bursa copulatrix absent or present; when present, varying in length. Window of bursa present in Diaperini. Vaginal sclerites present in Ectychini. Spermatheca present or absent; when present, reniform, spherical, spherical with invaginations (Diaperini), a coiled tube (Ectychini), or a portion of the accessory gland, but always inserted at the base of the accessory gland. Sternite VIII usually transverse, usually bearing spiculum ventrale anteriorly, apex truncate to rounded, covered with long setae. Spiculum ventrale usually as long as or longer than the ovipositor, reduced to a subtriangular sclerotization in Ectychini, and absent in Leiochrinini. Tergite VIII usually transverse, conspicuously formed by two plates, except in Hypophlaeini. Proctiger usually lanceolate, as long as ovipositor, bearing baculi laterally.

Diaperini: Adelinina

Alphitophagus bifasciatus (Say, 1823)

Figures 1–3

Gonocoxites (Fig. 2) about 1.5 times longer than wide. Paraprocts about as long as gonocoxites. Gonocoxites divided into 4 lobes ventrally. Basal lobes short, about 1/10 the length of ovipositor, bearing transverse baculi. Lobes 2 and 3 subequal in length, comprising together about 2/3 of the length of ovipositor. Apical lobe oblique, about 1/5 of the length of ovipositor. Gonostyli almost as long as apical lobe, inserted almost terminally, bearing an apical long seta surrounded by 5 small setae. Paraprocts bearing baculi, articulated almost at the central end of baculi of gonocoxites, arched laterally to middle, then parallel form middle to anterior end. Bursa copulatrix about 1.5 times as long as ovipositor, bearing a window anteriorly; window of bursa (Fig. 2) rounded, small, about 1/3 the length of spermatheca and 1/50 the length of bursa. Spermatheca (Fig. 3) about 1/3 as long as gonocoxites, spherical, inserted at base of spermathecal gland, almost anteriorly to bursa, bearing two invaginations. Invagination of spermatheca close to the bursa, reaching 1/3 of the spermatheca length; invagination far from bursa chalice like, expanding towards the spermathecal center, reaching the middle. Sternite VIII transverse, about 1.5 times as wide as long, bearing spiculum ventrale anteriorly, truncate apically, apex bearing long setae. Spiculum ventrale stick-like, about as long as ovipositor and parapropcts together. Tergite VIII transverse, about 1.5 times as wide as long, truncate anteriorly, bilobed at apex; each apex truncate, bearing long setae. Proctiger lanceolate, as long as gonocoxites, bearing baculi laterally.

Diaperini: Diaperina

Diaperis boleti (Linnaeus, 1758)

Figures 4–7

Gonocoxites (Fig. 5) transverse, about 1.25 times as wide as long. Paraprocts about twice as long as gonocoxites. Gonocoxites without distinct lobes; baculi transverse to middle, then oblique towards apex. Apex of coxites conspicuously sclerotized, with two apical teeth each (Fig. 5); area between teeth covered with setae, about 10 in each coxite. Gonostyli small, about 1/15 as long as gonocoxites, inserted dorso-laterally, bearing a long apical seta surrounded with small ones. Paraprocts bearing baculi, articulated at the middle of baculi of coxites, in the point that each coxite baculus curves towards apex. Baculi of paraprocts straight, slightly divergent. Bursa copulatrix about 2/3 as long as ovipositor, bearing a window anteriorly; window of bursa (Fig. 5) rounded, about 2/3 the length of spermatheca and 1/10 the length of bursa. Spermatheca (Fig. 7) about 1/5 as long as gonocoxites, spherical, inserted almost anteriorly to bursa, at the base of spermathecal gland, bearing two invaginations. Invagination of spermatheca close to bursa, reaching 1/3 of the spermatheca length; invagination far from bursa reaching 2/3 of the length of spermatheca, touching the other invagination; both invaginations cylindrical, with parallel sides. Sternite VIII transverse, about 3 times as wide as long, bearing spiculum ventrale anteriorly, truncate apically, apex bearing long setae. Spiculum ventrale (Fig. 6) bifurcate posteriorly, expanded anteriorly, about 1.5 times as long as ovipositor. Tergite VIII transverse, about 3 times as wide as long, composed by two conspicuously separated plates, apex of each plate covered by long setae. Proctiger lanceolate, about twice as long as gonocoxites, bearing baculi laterally, baculi expanded anteriorly.

Comments. This unusual morphology of gonocoxites was also observed by Doyen and Tschinkel (1982), who have not observed it in any other Tenebrionidae. However, similar morphology is found in four species of *Neomida* Latreille. In species of *Neomida* there is only one tooth, not as developed as the ones found in *Diaperis*, and the lobes of gonocoxites are still visible (Aloquio 2016). The enlargement of the proctigeral baculi is another odd feature of *Diaperis*, shared with *Phaleria*. The window of bursa seems to be a character found only in Diaperini, and its shape and length are heavily variable (e.g. Aloquio and Lopes-Andrade 2015, Aloquio 2016).

Gnathidiini

Menimus ovalis (Allard, 1894)

Figures 8–9

Gonocoxites (Fig. 9) about 1.25 times as long as wide. Paraprocts about half as long as gonocoxites. Gonocoxites divided into 4 lobes ventrally. Basal lobe about 1/6 of the length of gonocoxites, bearing slightly oblique baculi. Lobe 2 as long as basal lobe. Lobes 3 and 4 partially fused, subequal in length. Apical lobe oblique, heavily sclerotized, bearing long setae apically surrounding gonostyli. Gonostyli about 1/6 as long as gonocoxites, inserted apically, bearing long setae all over its surface. Paraprocts bearing baculi, articulated almost at the central end of baculi of coxites, arched laterally. Bursa copulatrix and spermatheca absent. Accessory gland bifurcate (Fig. 9), inserted at the anterior end of vagina. Sternite VIII transverse, about 3.5 times as wide as long, bearing the spiculum ventrale anteriorly, truncate at apex, apex covered with long setae. Spiculum ventrale stick-like, about 1.5 times as long as ovipositor, suture visible. Tergite VIII transverse, about 2.25 times as wide as long, formed by two conspicuously separate plates, apex covered with long setae. Proctiger subtriangular, about half as long as ovipositor, bearing baculi laterally.

Comments. The bifurcate accessory gland is an unusual feature within Tenebrionidae. We found no information on the occurrence of this feature in other species of Gnathidiini. The gonostyli bearing long setae in all its length is another feature that differs *Menimus* from other Diaperinae.

Hypophlaeini

Corticeus unicolor (Piller & Mitterpacher, 1783)

Figures 10–12

Gonocoxites (Fig. 11) about 1.5 times as long as wide. Paraproct about half as long as gonocoxites. Gonocoxites divided into 4 lobes ventrally. Basal lobe about 1/5 the length of gonocoxites, bearing baculi oblique to middle, then transverse; baculi expanding to center end. Lobes 2 and 3 subequal in length. Apical lobe transverse, as long as lobes 2 and 3 together, heavily sclerotized. Gonostyli 1/10 as long as gonocoxites, inserted terminally, bearing a long seta surrounded by small ones apically. Paraprocts bearing baculi, articulated almost at the central end of baculi of coxites, diverging from each other from the posterior end to middle, then slightly converging anteriorly. Bursa copulatrix about 1.25 times as long as ovipositor. Spermatheca (Fig. 12) about 2/5 as long as gonocoxites, spherical, thin-walled, inserted at the middle of bursa by a thin canal, linked to the enlarged apical gland. Sternite VIII subquadrate, as long as wide, bearing the spiculum ventrale anteriorly, rounded apically, apex covered with long setae. Spiculum ventrale as long as gonocoxites, bilobed posteriorly, each lobe directed laterally, strait anteriorly, expanding to anterior 1/3. Tergite VIII subquadrate, as long as wide, slightly truncate at apex, apex covered with long setae. Proctiger lanceolate, about 2/3 as long as ovipositor, bearing baculi laterally.

Leiochrinini

Leiochrinus sauteri Kaszab, 1946

Figures 13–15

Gonocoxites (Fig. 14) transverse, about twice as wide as long. Paraprocts about half as long as gonocoxites. Gonocoxites divided into 2 lobes ventrally. Basal lobe twice as long as apical lobe, bearing oblique, almost parallel baculi. Apical lobe bearing long setae apically. Gonostyli about 1/5 as long as gonocoxites, inserted apically, bearing a long seta apically, surrounded by small ones. Paraproct bearing baculi, articulated with anterior end of baculi of coxites; paraprocts inserted almost laterally to coxites. Bursa copulatrix absent. Spermatheca (Fig. 15) reniform, thin walled, inserted anteriorly to vagina. Sternite VIII transverse, about 3.5 times as wide as long, truncate anteriorly, slightly rounded apically, apex covered with long setae. Spiculum ventrale absent. Tergite VIII transverse, about 3.5 times as wide as long, formed by two conspicuously separate plates, apex covered with long setae. Proctiger not observed.

Comments. The gonocoxites of *Leiochrodes sauteri* is very similar to that of *Nilio* (*Nilio*) *brunneus* Thomson, 1860 (Nilioninae) (e.g. Aloquio and Lopes-Andrade 2016). This could be due to the fact that both species lay eggs in a similar substrate (tree barks, close to lichens), not due to an evolutionary proximity, an assumption that is supported by the very different spermatheca. The absence of spiculum ventrale may be due to the reduction of the gonocoxites, which is also observed in *N. brunneus*.

Myrmechixenini

Myrmechixenus vaporariorum Guérin-Méneville, 1843

Figures 16–17

Gonocoxites (Fig. 17) subquadrate, as long as wide. Paraprocts about 2/3 as long as gonocoxites. Gonocoxites divided into 3 lobes ventrally. Lobes subequal in length. Basal lobes bearing thick, transverse baculi. Apical lobes truncate at apex. Gonostyli about 1/4 as long as gonocoxites, inserted terminally, apex bearing a long seta surrounded by small ones. Paraprocts bearing baculi, articulated almost at the central end of baculi of coxites, arched laterally, together forming a U-shape. Bursa copulatrix and spermatheca not observed. Sternite VIII transverse, about 3.25 times as wide as long, bearing the spiculum ventrale anteriorly, rounded posteriorly, apex covered with long setae. Spiculum ventrale about 4/5 as long as ovipositor Y to T-shaped, bilobed posteriorly, lobes directed laterally almost at 180º from each other, strait anteriorly. Tergite VIII transverse, about 3 times as wide as long, rounded posteriorly, apes covered with long setae. Proctiger trapezoidal, 1.5 times as long as gonocoxites, bearing baculi laterally, baculi converging to apex.

Scaphidemini

Scaphidema metallicum (Fabricius, 1792)

Figures 18–20

Gonocoxites (Fig. 19) slender, about twice as long as wide. Paraprocts about 4/5 as long as gonocoxites. Gonocoxites divided into 4 lobes ventrally. Basal lobe short, about 1/10 the length of gonocoxites, bearing oblique baculi, baculi heavily sclerotized from middle to central end. Lobes 2 and 3 subequal in length. Apical lobe short, about 1/6 the length of gonocoxites, bearing long setae apically. Gonostyli about 1/6 as long as gonocoxites, inserted apically, bearing a long seta at apex surrounded by 5 small setae. Paraprocts bearing baculi, articulated at 1/3 central end of baculi of coxites, diverging to anterior 1/3, then converging, narrowing towards anterior end. Bursa copulatrix absent. Spermatheca (Fig. 20) reniform, inserted to vagina by a long tubular accessory gland. Sternite VIII transverse, about 1.25 times as wide as long, bearing the spiculum ventrale anteriorly, rounded apically, apex covered with long setae. Spiculum ventrale about as long as gonocoxites, Y-shaped, posterior end bilobed, lobes enlarging towards lateral, each lobe projecting anteriorly, fusing together at 1/3 anterior end. Proctiger lanceolate, about 3/4 as long as ovipositor, bearing baculi laterally, baculi enlarging from middle to apex.

Incertae sedis

Triplehornia metallica Matthews and Lawrence, 2005

Figures 21–23

Gonocoxites (Fig. 22) about twice as long as wide. Paraprocts about half as long as gonocoxites. Gonocoxites divided into 4 lobes ventrally. Basal lobes subequal in length with lobes 3 and 4, bearing oblique baculi, baculi converging anteriorly, touching each other at the central end. Lobe 2 about 1/3 of the length of gonocoxites. Lobes 3 and 4 partially fused. Apical lobe oblique, slightly sclerotized. Gonostyli about 1/6 as long as gonocoxites, heavily sclerotized, inserted apically, apex bearing a long seta surrounded by small ones. Paraprocts bearing baculi, articulated almost at the central end of baculi of coxites, almost strait, converging from each other, narrowing anteriorly. Bursa copulatrix (Fig. 22) about 3/4 as long as gonocoxites. Vagina enlarged at anterior 1/3 (Fig. 23). Accessory gland inserted anteriorly to enlargement of vagina (Fig. 23). Spermatheca absent. Sternite VIII transverse, about 2.25 times as wide as long, bearing the spiculum ventrale anteriorly, apex truncate, covered with long setae. Spiculum ventrale about 4/5 as long as ovipositor, Y to T-shaped, posterior lobes diverging from each other in almost 180º, suture conspicuous. Tergite VIII transverse, about 2.25 times as wide as long, truncate anterior and posteriorly, apex covered with long setae. Proctiger lanceolate, as long as gonocoxites, bearing baculi laterally.

Comments. The bursa copulatrix as an appendage of the vagina resembles that of *Trachyscelis* (Trachyscelini). The enlarged anterior end of the vagina, with the accessory gland attached, resembles that of *Menimus* (Gnathidiini). The gonocoxites, paraprocts, tergite VIII and sternite VIII and spiculum ventrale are similar to those found in *Scaphidema* (Scaphidemini). Morphological features of exposed structures do not shed light on the phylogenetic affinities of *Triplehornia* (Matthews and Bouchard 2008). Given that such modification of bursa could arise independently more than once, the morphology of the female abdominal terminalia may support that *Triplehornia*, in fact, belongs to the diaperine lineage within Diaperinae, not the phaleriine lineage.

Phaleriines

Phaleriini

Phaleria testacea Say, 1824

Figures 24–26

Gonocoxites (Figs 25–26) about 1.25 times as long as wide. Paraprocts about 2/3 as long as gonocoxites. Gonocoxites divided into 2 lobes ventrally. Basal lobe small, about 1/10 the length of gonocoxites, bearing thick, transverse baculi. Apical lobe obliquely sclerotized, narrowing abruptly form middle to apex, forming a long, slender inner projection (Fig. 26). Gonostyli about 1/10 as long as gonocoxites, inserted laterally at the middle of projection of apical gonocoxite, bearing a long seta apically surrounded by small ones. Paraprocts bearing baculi, articulated at 1/3 central end of baculi of coxites, diverging to middle, then parallel, narrowing to anterior end. Bursa copulatrix not observed. Spermatheca at basal 1/4 of accessory gland. Accessory gland (Fig. 25) about 4/5 as long as ovipositor. Sternite VIII transverse, about twice as wide as long, bearing the spiculum ventrale anteriorly, truncate at apex, apex covered with long setae. Spiculum ventrale about half as long as ovipositor, subtriangular at posterior end, stick like anteriorly, enlarging towards anterior end. Tergite VIII transverse, about twice as wide as long, formed by two conspicuously separate plates, apex covered with long setae. Proctiger (Fig. 26) lanceolate, about as long as ovipositor, bearing baculi laterally, baculi enlarged at anterior and posterior ends.

Comments. The morphology of the gonocoxites, with the long, narrow, sclerotized projections of apical lobes of gonocoxites, may appear odd in comparison to other diaperines. But this could be easily explained by the biology of *Phaleria*, which lives in costal dunes and lay eggs burying them in the sand. The morphology of the spermatheca observed in *Phaleria* is considered to be the primitive state of the structure in Diaperinae (Doyen and Tschinkel 1982).

Crypticini

Crypticus quisquilius (Linnaeus, 1760)

Figures 27–28

Gonocoxites (Fig. 28) subquadrate, as long as wide. Paraprocts about 0.25 as long as gonocoxites. Gonocoxites divided into 3 lobes ventrally. Lobes subequal in length. Basal coxite lobe bearing baculi, baculi oblique, converging anteriorly, touching each other at the central end. Apical lobes oblique, bearing inner protuberances as long as gonostyli.

Gonostyli about 1/5 the length of gonocoxites, inserted laterally, bearing two long setae apically, surrounded with small ones. Paraprocts bearing baculi, articulated almost at the central end of baculi of coxites; baculi of paraprocts strongly diverging from each other, forming an angle of almost 180º between them. Bursa copulatrix twice as long as ovipositor. Spermatheca absent. Sternite VIII transverse, twice as wide as long, bearing the spiculum ventrale anteriorly, rounded at apex, apex bearing long setae. Spiculum ventrale Y-shaped, bilobed posteriorly, each lobe reaching the lateral of the sternite VIII; strait towards anterior, expanded at the very tip; about 2/3 as long as ovipositor. Tergite VIII transverse, about twice as wide as long, formed by two conspicuously distinct plates, apex covered by long setae. Proctiger not observed.

Ectychini

Ectyche tuberculipennis Bates, 1873

Figures 29–31

Gonocoxites (Fig. 30) transverse, about 1.5 times as wide as long. Paraprocts half as long as gonocoxites. Gonocoxites divided into 3 lobes ventrally. Lobes 1 and 2 subequal in length. Basal lobes bearing oblique baculi. Apical lobe small, about 1/10 the length of gonocoxites. Gonostyli about 1/10 as long as gonocoxites, inserted apically, bearing a long seta apically surrounded by small ones. Paraprocts bearing baculi, articulated 1/3 the central end of baculi of coxites, diverging from each other almost at a 180º; paraprocts inserted almost laterally to coxites. Bursa copulatrix (Fig. 30) about twice as long as ovipositor. Vagina bearing a sclerite at midpoint from basal lobe of coxites to insertion of common oviduct; vaginal sclerite as long as gonostyli. Spermatheca (Fig. 31) tubular, coiled, inserted close to the common oviduct by a long tubular portion of the accessory gland. Sternite VIII transverse, about 2.5 times as wide as long, bearing the spiculum ventrale anteriorly, apex rounded, covered with long setae. Spiculum ventrale subtriangular, short, about 1/5 as long as gonocoxites. Tergite VIII transverse, about 2.5 times as wide as long, apex truncate, covered with long setae, anterior end of lateral edges sclerotized. Proctiger lanceolate, as long as ovipositor, bearing baculi laterally.

Comments. The morphology of the spermatheca in *Ectyche* resembles that of Lagriinae, differing only in the anatomical origin. The spermatheca in *Ectyche* is a modification of a portion of the accessory gland, while in Lagriinae the spermatheca arises directly from the bursa. The modifications in the ovipositor can be explained by its xeric, soil inhabiting biology.

Hyociini

Csiro variegata (Blackburn, 1894)

Figures 32–33

Gonocoxites (Fig. 33) transverse, about 1.5 times as wide as long. Paraprocts about 1.5 times as long as gonocoxites. Gonocoxites without conspicuous lobes. Gonocoxites with oblique baculi, baculi arched towards anterior end. Gonostyli absent. Paraprocts bearing thick, parallel baculi, articulated at middle of baculi of coxites. Bursa copulatrix (Fig. 33) about 1.5 times as long as ovipositor. Spermatheca absent. Sternite VIII transverse, about 1.5 times as wide as long, bearing the spiculum ventrale anteriorly, rounded at apex, apex covered with long setae, sclerotized laterally. Spiculum ventrale T-shaped, about half as long as ovipositor, enlarged posteriorly, with points towards lateral of sternite VIII, strait to anterior end, suture visible to middle. Tergite VIII transverse, about 1.5 times as wide as long, formed by two conspicuously separate plates, apex covered with long setae, apex of lateral edges sclerotized. Paraproct lanceolate, about 4/5 as long as ovipositor, bearing baculi laterally.

Trachyscelini

Trachyscelis pallens Champion, 1893

Figures 34–35

Gonocoxites (Fig. 35) transverse, about twice as wide as long. Paraprocts as long as gonocoxites. Gonocoxites without conspicuous lobes. Gonocoxites bearing oblique baculi. Gonostyli absent. Paraprocts bearing thick baculi, articulated with the middle of baculi of coxites, diverging from each other. Bursa copulatrix (Fig. 35) about 2.5 times as long as ovipositor, separated from vagina by a constriction. Spermatheca absent. Auxiliary gland (Fig. 35) attached to vagina near common oviduct, apical 1/3 glandular. Eight sternite transverse, about 3 times as wide as long, bearing the spiculum ventrale anteriorly, apex rounded, covered with long setae. Spiculum ventrale stick like, enlarging anteriorly, as long as gonocoxites and paraprocts together. Tergite VIII transverse, about twice as wide as long, apex truncate, covered by long setae, sclerotized laterally. Proctiger not observed.

Discussion

Diaperinae is believed to be divided into two major informal groups (*sensu* Matthews and Bouchard 2008), the 'diaperine Diaperinae', comprising Diaperini, Gnathidiini, Hypophlaeini, Leiochrinini, Myrmechixenini, Scaphidemini and *Triplehornia*, and the 'phaleriine Diaperinae', comprising Phaleriini, Crypticini, Ectychini, Hyociini and Trachyscelini. These two groups are defined mainly by the habitats that they occupy, with the former living in forests and the later in edaphic soils or deserts. There are also differences in morphology, as the female abdominal terminalia, which is assumed to be primitive in phaleriine (Matthews and Bouchard 2008). In fact, there are quite a few differences, most of them in the ovipositor, usually reduced in phaleriines and fully formed, unmodified of the primitive type for the family in diaperines. However, it shall be noted that the morphology of the ovipositor may be a consequence of habitat convergence. For instance, reduced ovipositor occurs in most tenebrionids that oviposit in soil, leading to a tautology when this feature is used as an additional argument for separating the edaphic or desert phaleriines from the other Diaperinae. Other differences are found in the labrum, with the clypeolabral membranes covered in phaleriines and exposed in diaperines (Matthews and Bouchard 2008), also could be explained by the similar diets, and internal tract structures of female abdominal terminalia, which could have arisen independently several times (Doyen and Tschinkel 1982, Tschinkel and Doyen 1980). Therefore, the morphology of female abdominal terminalia alone does not sustain these informal groups.

The ovipositor has a high degree of autapormophies (e.g. *Diaperis, Phaleria*) and its morphology depends highly on the substrate in which the eggs are deposited (e.g. *Leiochrodes*, *Nilio*, *Csiro, Trachyscelis*) (Doyen and Tschinkel 1982). Therefore, its phylogenetic signal may be low. But structures such as the spermatheca and the bursa copulatrix possibly have great phylogenetic signal and we recommend including information on their morphology in descriptions of Diaperinae and even of other tenebrionids, because we think the morphology of these structures may shed light on the higher classification of the family. Aside from probably having low phylogenetic signal, the morphology of female abdominal terminalia as a whole is important to be included in species' descriptions, since they provide great diagnostic features between species within a genus. We have already had great results in resolving morphological limits between species of *Neomida*, in which females are virtually identical externally (Aloquio 2016).

The female reproductive tract of Diaperinae provides great diagnostic features (Doyen and Tschinkel 1982) and, based on the present paper, for all the taxa currently included in Diaperinae. The capsular spermatheca is a distinctive feature of diaperine and outside diaperine it occurs only in *Nilio* (Aloquio & Lopes-Andrade 2016), which is considered to be within the lagrioid branch, but previously it was considered closely related to Diaperini (Doyen and Tschinkel 1982).

We did not find any data to help solving the position of *Triplehornia* and we shall leave it as incertae sedis. *Triplehornia* shares features especially with Scaphidemini and Gnathidiini, and it either deserves a tribe of its own or to be included in a tribe resulted from the fusion of Scaphidemini and Gnathidiini.

List of characters with possible phylogenetic signal

Characters of phylogenetic relevance are listed below. The character states for all taxa studied are presented in the table 1.

1. Spermatheca: present (0); absent (1).
2. Spermatheca, shape: spherical (0); reniform (1); tubular (2).
3. Spermatheca, invaginations: present (0); absent (1).
4. Gonocoxites, proportions: transverse (0); subquadrate (1); lengthwise (2).
5. Gonocoxites, ventral lobes: conspicuously visible (0); not visible (1).
6. Gonocoxites, number of ventral lobes: 4 (0); 3 (1); 2 (2).
7. Gonocoxites, modifications at apex: without modifications (0); teeth* (1); long, narrow projection* (2).
8. Baculi of gonocoxites, relative to gonocoxites: oblique (0); transverse (1); parallel (2).
9. Gonostyli: present (0); absent (1).
10. Gonostyli, insertion relative to apical lobe of gonocoxites: apical (0); lateral (1); dorso-lateral (2).
11. Spiculum ventrale: present (0); absent (1).
12. Spiculum ventrale, length relative to length of ovipositor: as long as (0); longer (1); much shorter (2).
13. Bursa copulatrix: present (0); absent (1).
14. Bursa copulatrix, length relative to length ovipositor: as long as (0); longer (1); shorter (2).
15. Bursa copulatrix, window: present (0); absent (1).
16. Accessory gland, if bifurcate or not: not bifurcate (0); bifurcate* (1).
17. Vagina, sclerites: present (0); absent (1).
18. Paraprocts, length relative to ovipositor: as long as (0); shorter (1); longer (2).
19. Paraprocts, baculi orientation relative to ovipositor: parallel (0); oblique (1).

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* Character states observed only in the studied genus within the tribe and not mentioned in literature or observed by us in any other genus.

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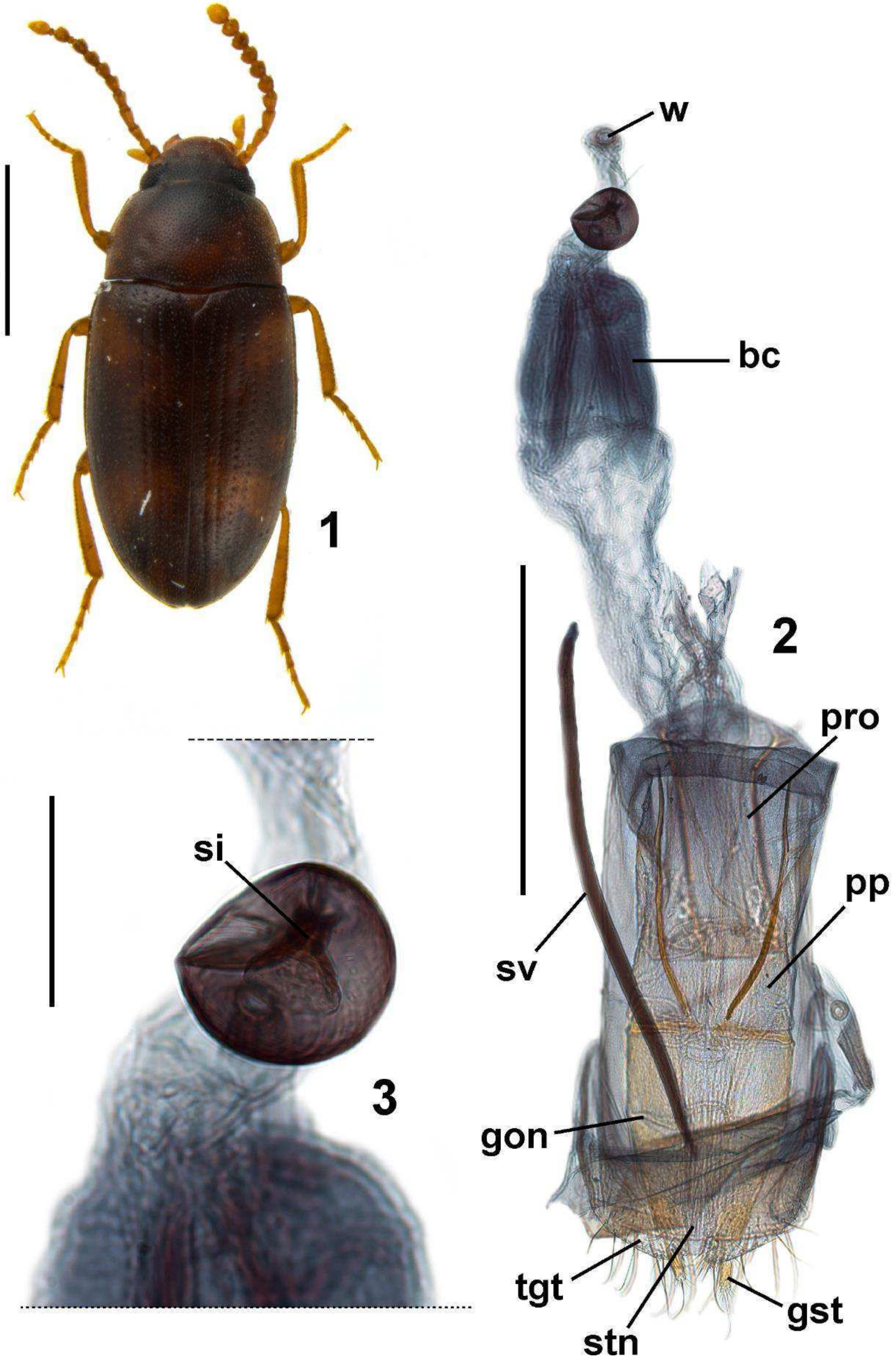
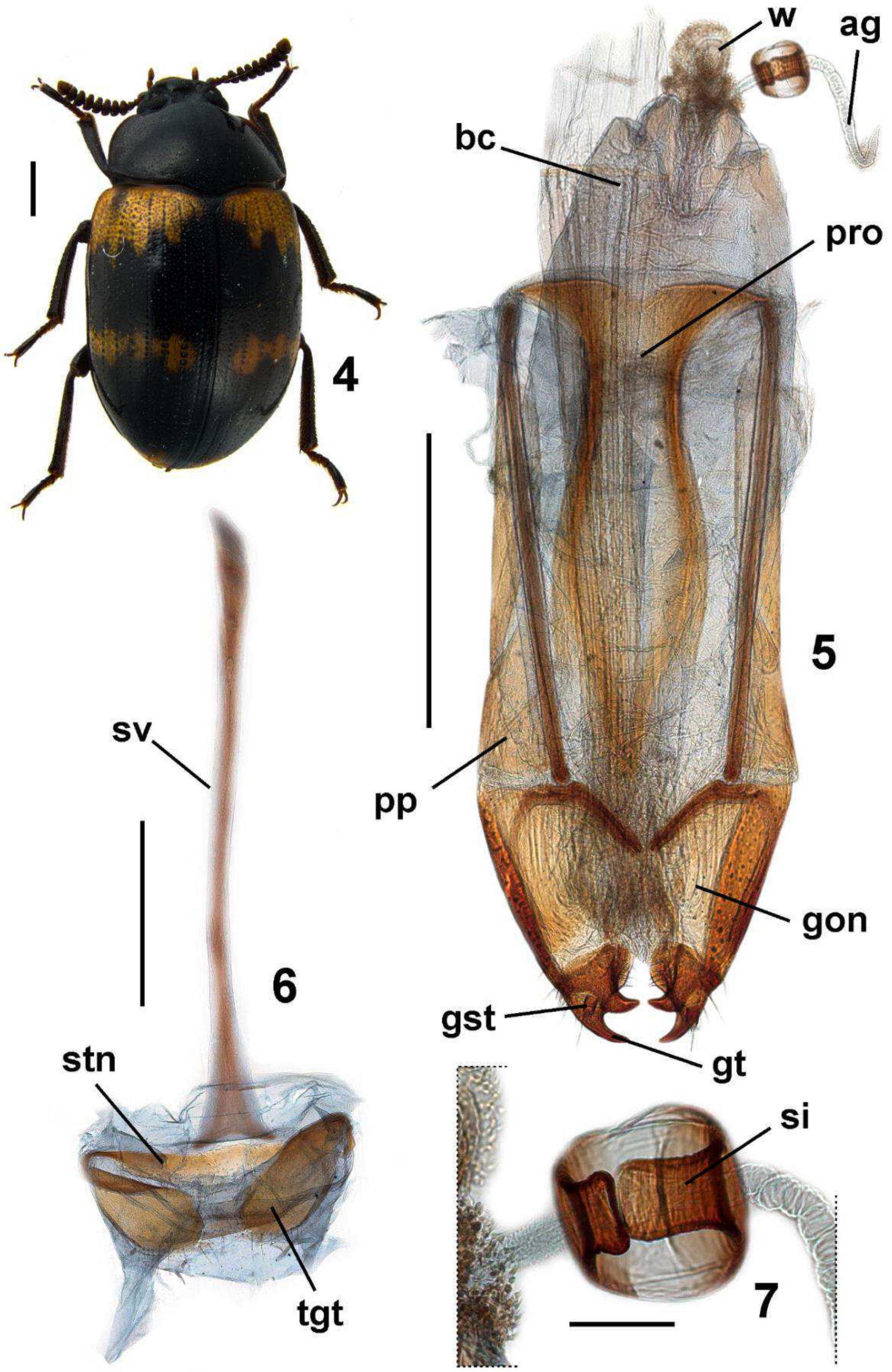
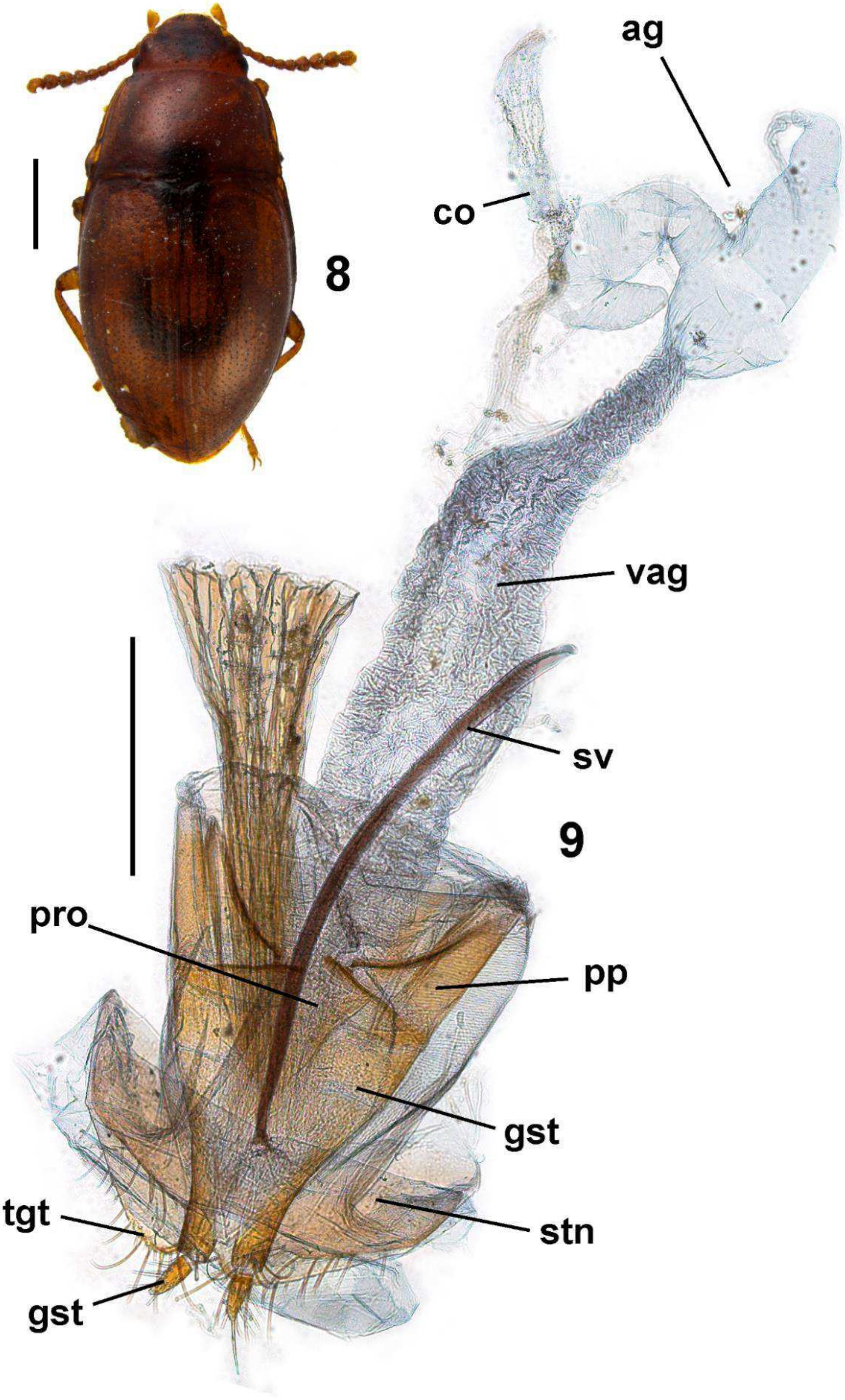


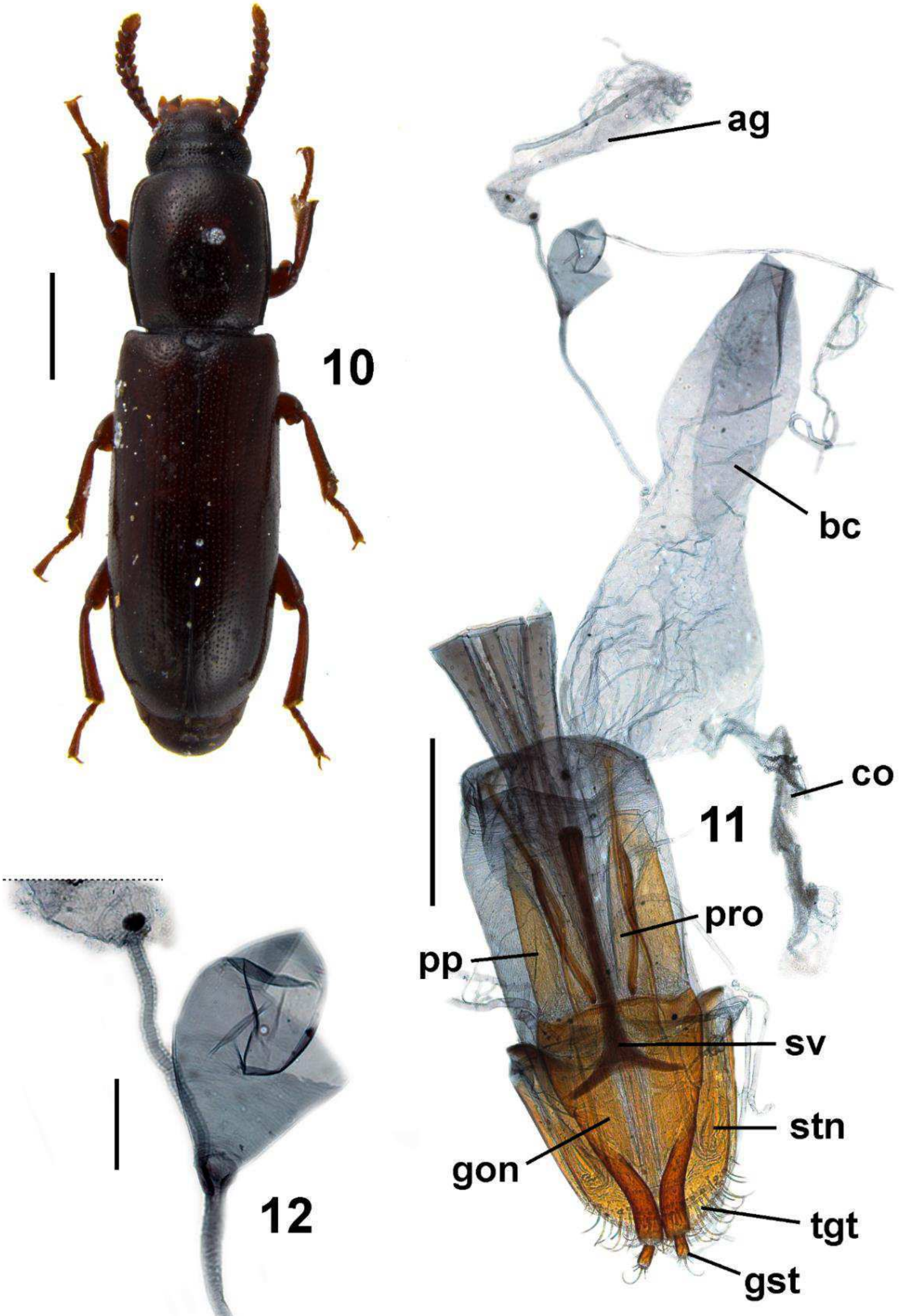
Figures 1–3. *Alphitophagus bifasciatus*, (1) dorsal view, (2) female abdominal terminalia and (3) spermatheca. **bc** – bursa copulatrix, **gon** – gonocoxite, **gst** – gonostylus, **pp** – paraproct, **pro** – proctiger, **si** – spermathecal invaginations, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII, **w** – window of bursa. Scale bar: 1 mm (Fig. 1), 0.5 mm (Fig. 2) and 0.1 mm (Fig. 3).



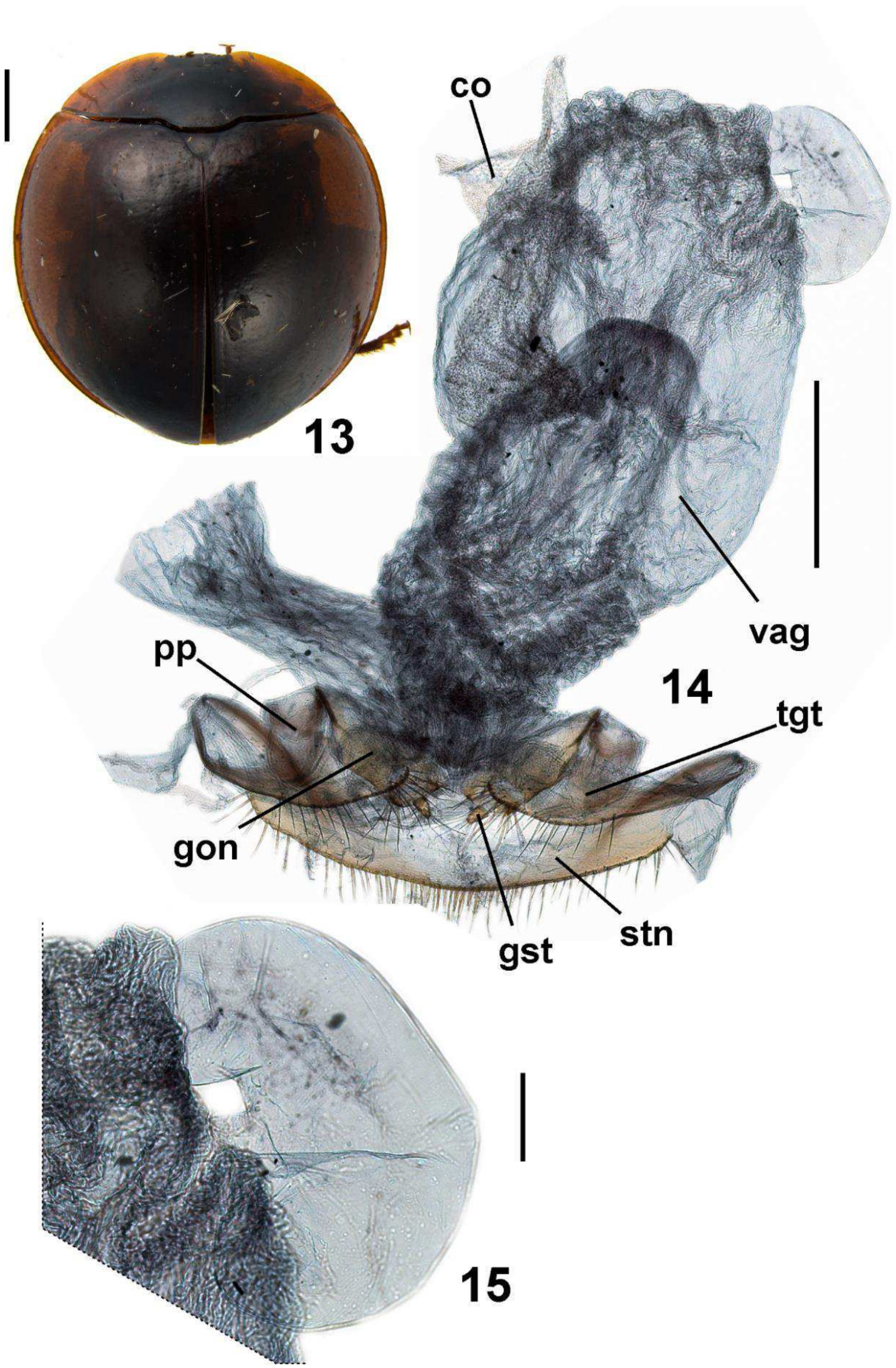
Figures 4–7. *Diaperis boleti*, (4) dorsal view, (5) female abdominal terminalia, (6) spiculum ventrale and (7) spermatheca. **ag** – accessory gland, **bc** – bursa copulatrix, **gon** – gonocoxite, **gst** – gonostylus, **gt** – tooth of gonocoxite, **pp** – paraproct, **pro** – proctiger, **si** – spermathecal invaginations, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII, **w** – window of bursa. Scale bar: 1 mm (Figs 4–6) and 0.1 mm (Fig. 7).



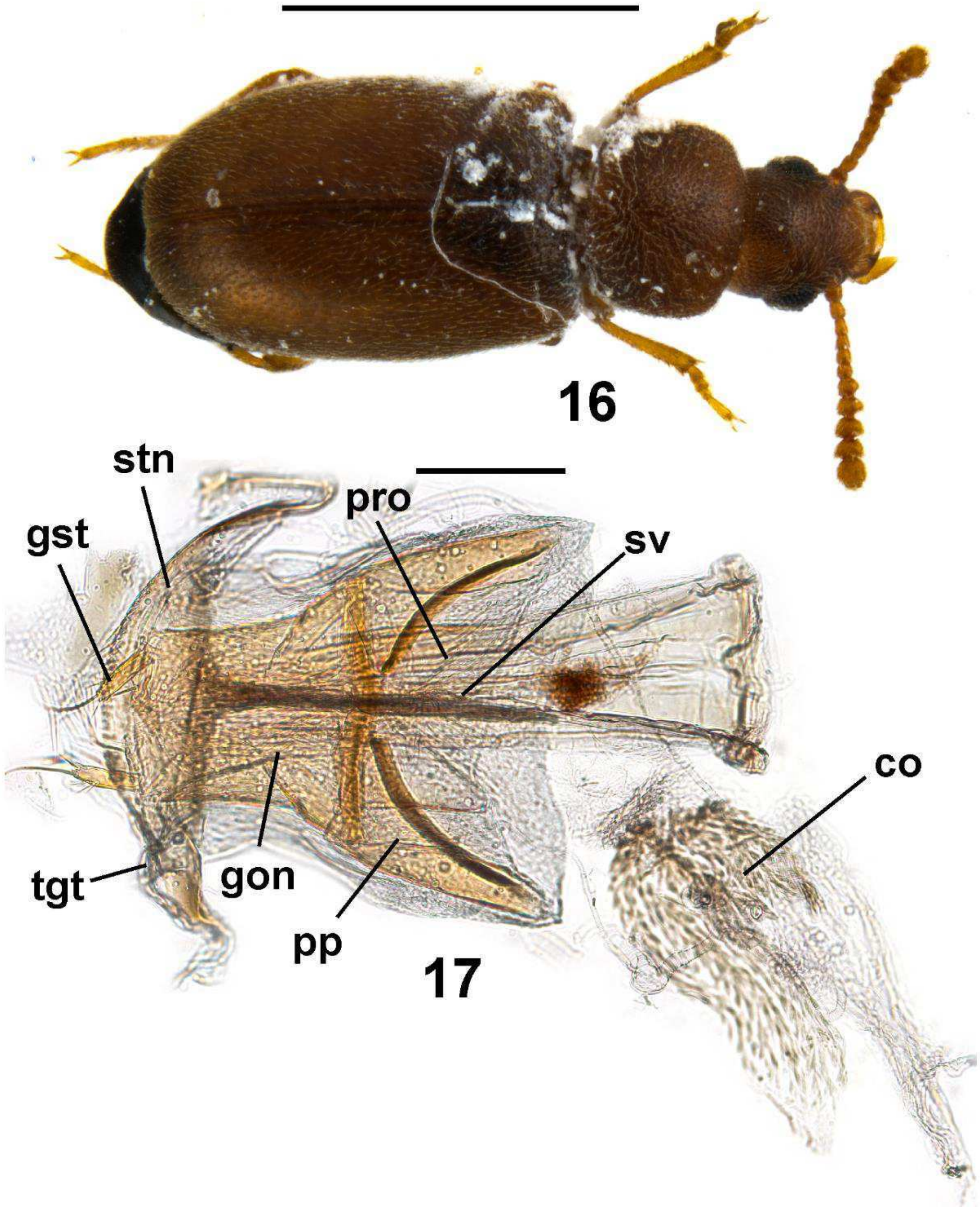
Figures 8–9. *Menimus ovalis*, (8) dorsal view and (9) female abdominal terminalia. **ag** – accessory gland, **bc** – bursa copulatrix, **co** – common oviduct, **gst** – gonostylus, **pp** – paraproct, **pro** – proctiger, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII, **vag** – vagina. Scale bar: 1 mm (Fig. 8) and 0.5 mm (Fig. 9).



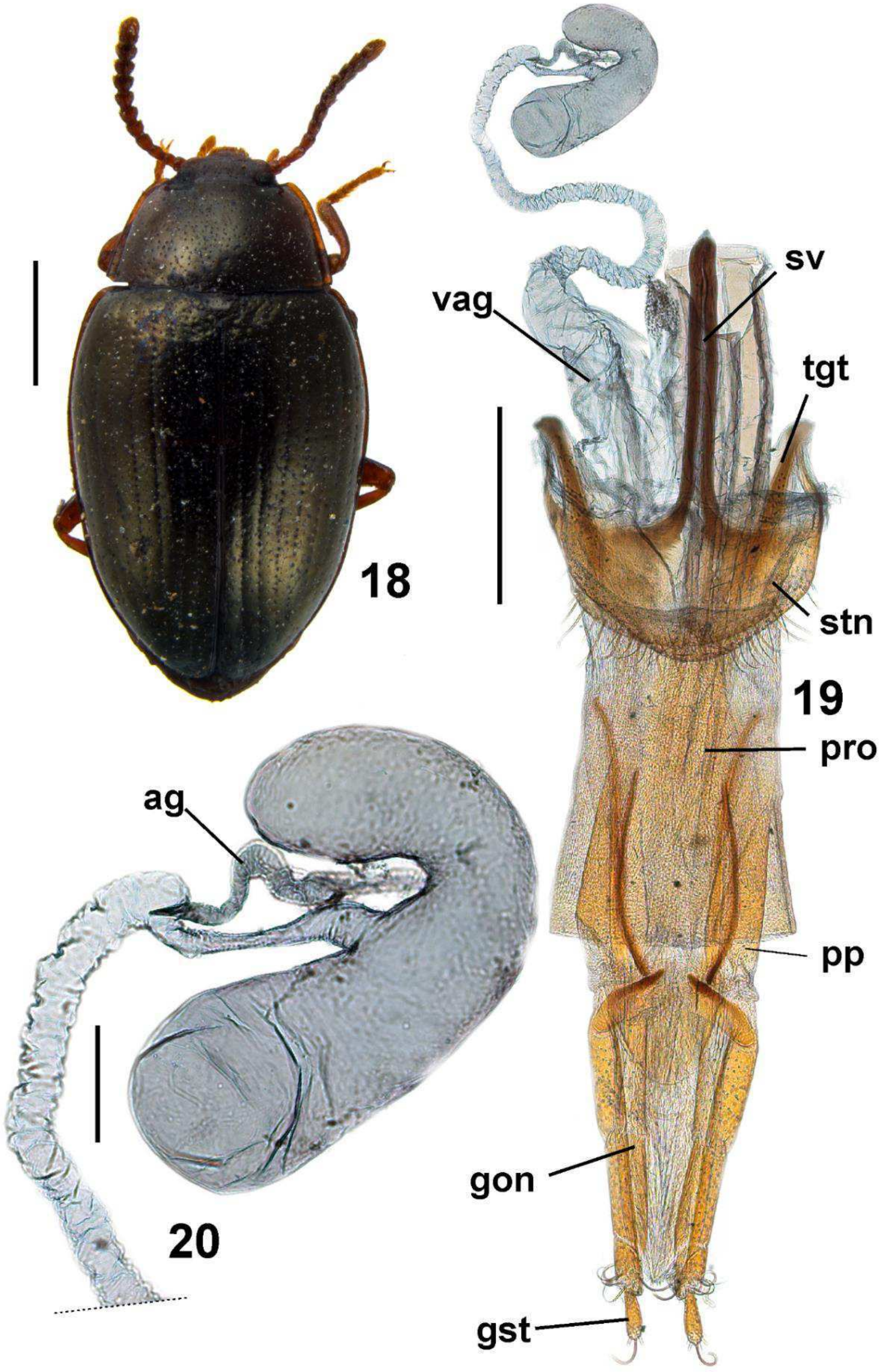
Figures 10–12. *Corticeus unicolor*, (10) dorsal view, (11) female abdominal terminalia and (12) spermatheca. **ag** – accessory gland, **bc** – bursa copulatrix, **co** – common oviduct, **gon** – gonocoxite, **gst** – gonostylus, **pp** – paraproct, **pro** – proctiger, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII. Scale bar: 1 mm (Fig. 10), 0.5 mm (Fig. 11) and 0.1 mm (Fig. 12).



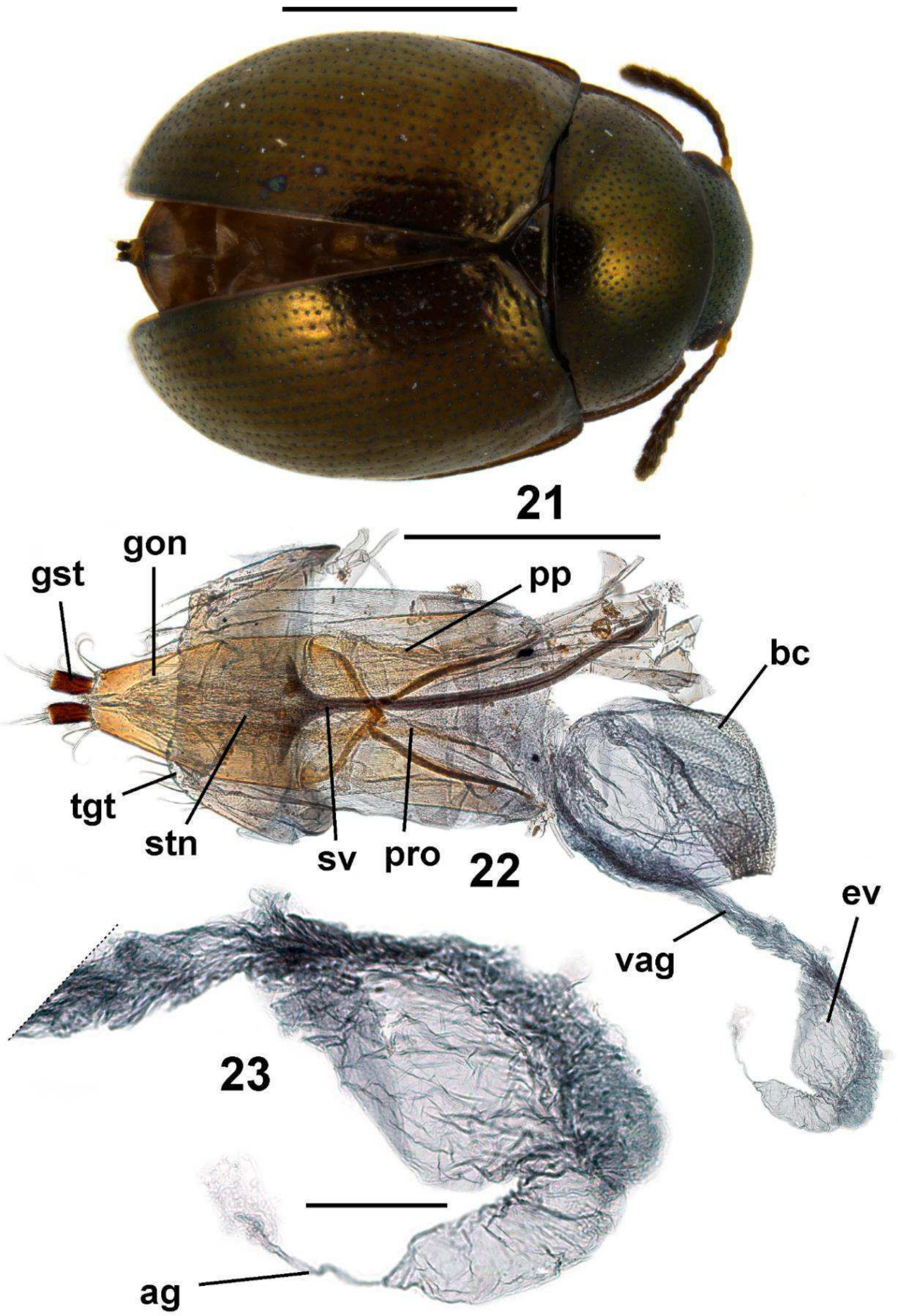
Figures 13–15. *Leiochrinus sauteri*, (13) dorsal view, (14) female abdominal terminalia and (15) spermatheca. **co** – common oviduct, **gon** – gonocoxite, **gst** – gonostylus, **pp** – paraproct, **sp** – spermatheca, **stn** – sternite VIII, **tgt** – tergite VIII, **vag** – vagina. Scale bar: 1 mm (Fig. 13), 0.5 mm (Fig. 14) and 0.1 mm (Fig. 15).



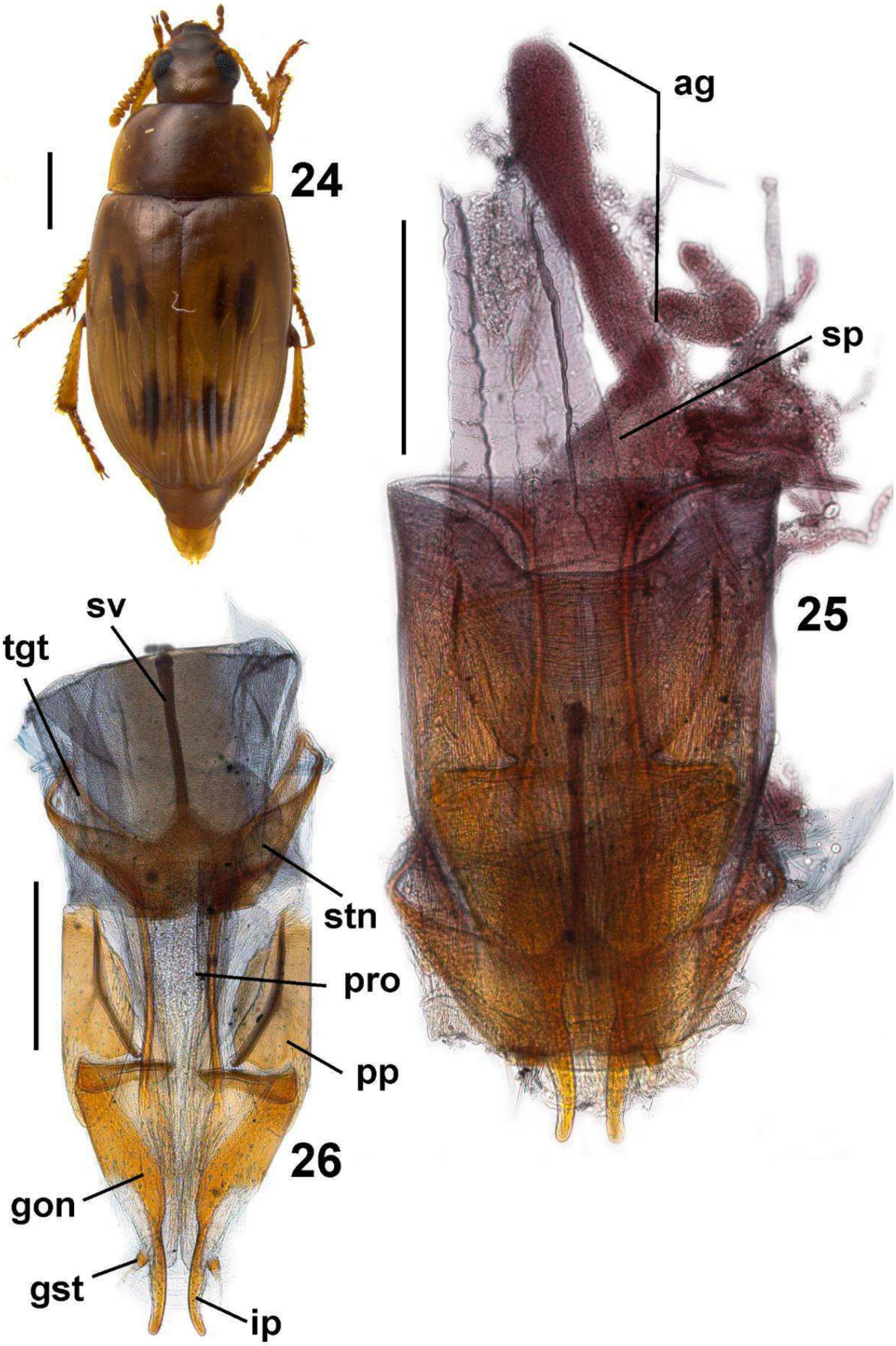
Figures 16–17. *Myrmechixenus vaporariorum*, (16) dorsal view and (17) ovipositor. **co** – common oviduct, **gon** – gonocoxite, **gst** – gonostylus, **pp** – paraproct, **pro** – proctiger, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII. Scale bar: 1 mm (Fig. 16) and 0.1 mm (Fig. 17).



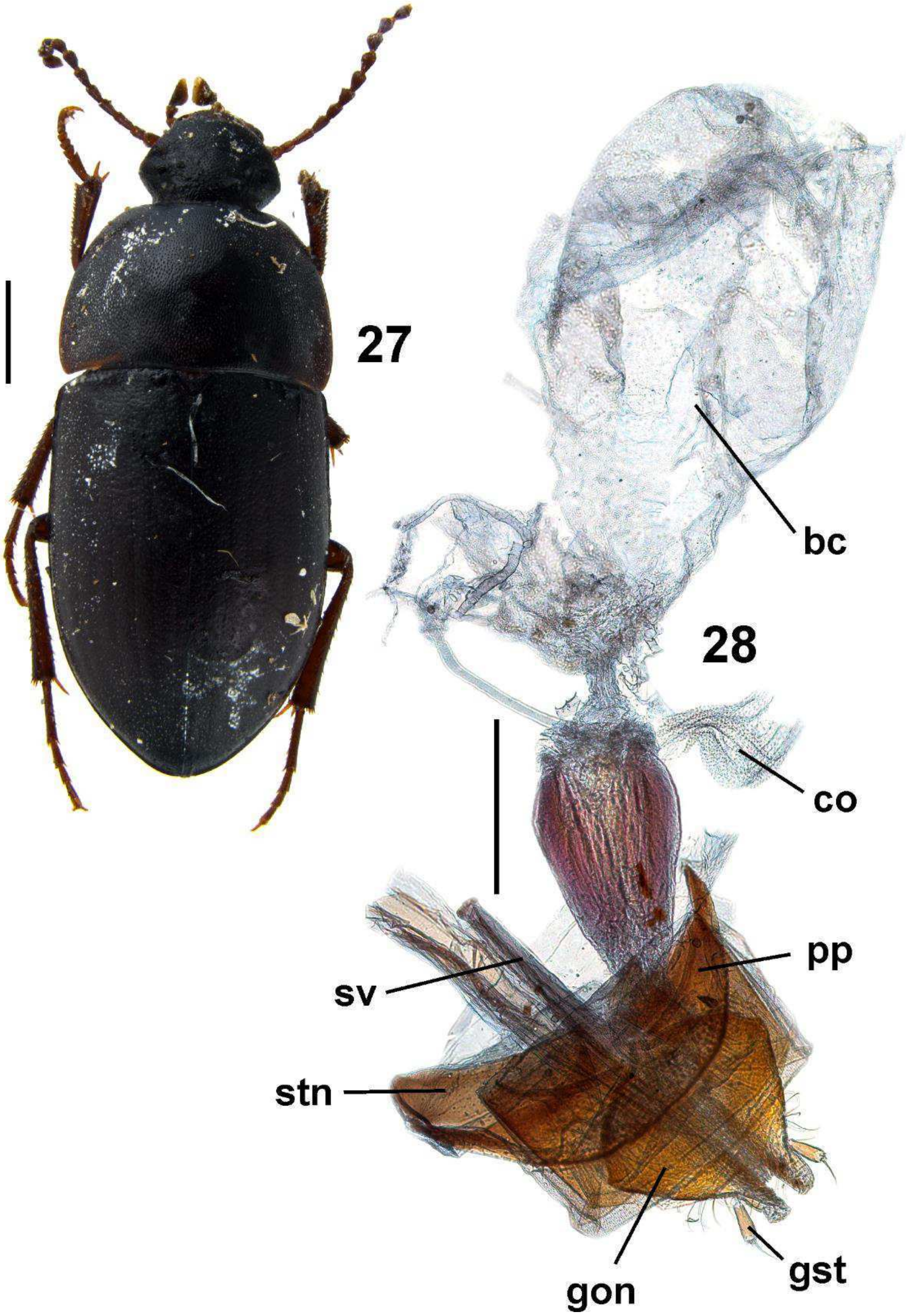
Figures 18–20. *Scaphidema metallicum*, (18) dorsal view, (19) female abdominal terminalia and (20) spermatheca. **ag** – accessory gland, **gon** – gonocoxite, **gst** – gonostylus, **pp** – paraproct, **pro** – proctiger, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII, **vag** – vagina. Scale bar: 1 mm (Fig. 18), 0.5 mm (Fig. 19) and 0.1 mm (Fig. 20).



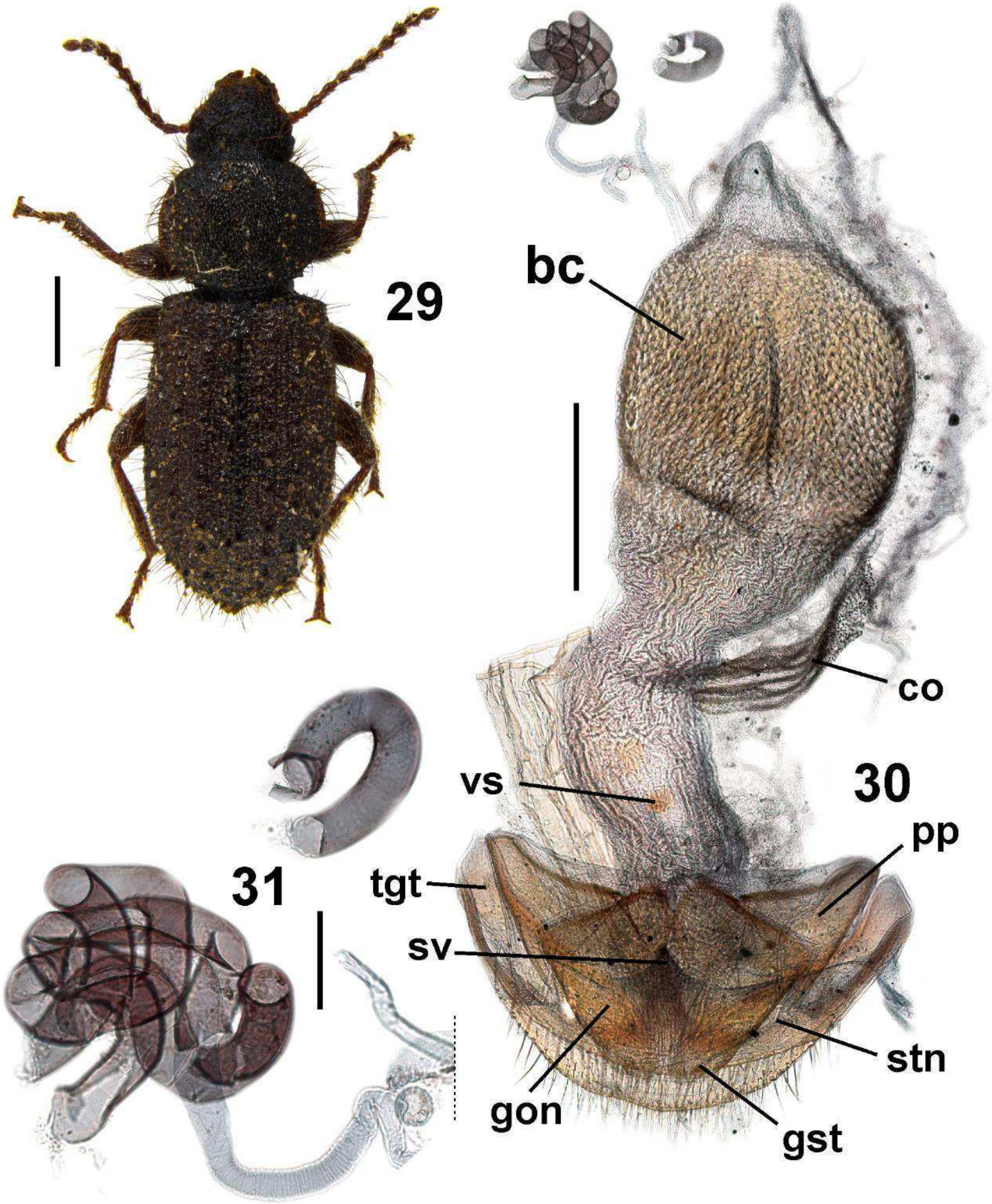
Figures 21–23. *Triplehornia metallica*, (21) dorsal view, (22) female abdominal terminalia and (23) enlargement of vagina. **ag** – accessory gland, **bc** – bursa copulatrix, **ev** – enlargement of vagina, **gon** – gonocoxite, **gst** – gonostylus, **pp** – paraproct, **pro** – proctiger, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII, **vag** – vagina. Scale bar: 1 mm (Fig. 21), 0.5 mm (Fig. 22) and 0.1 mm (Fig. 23).



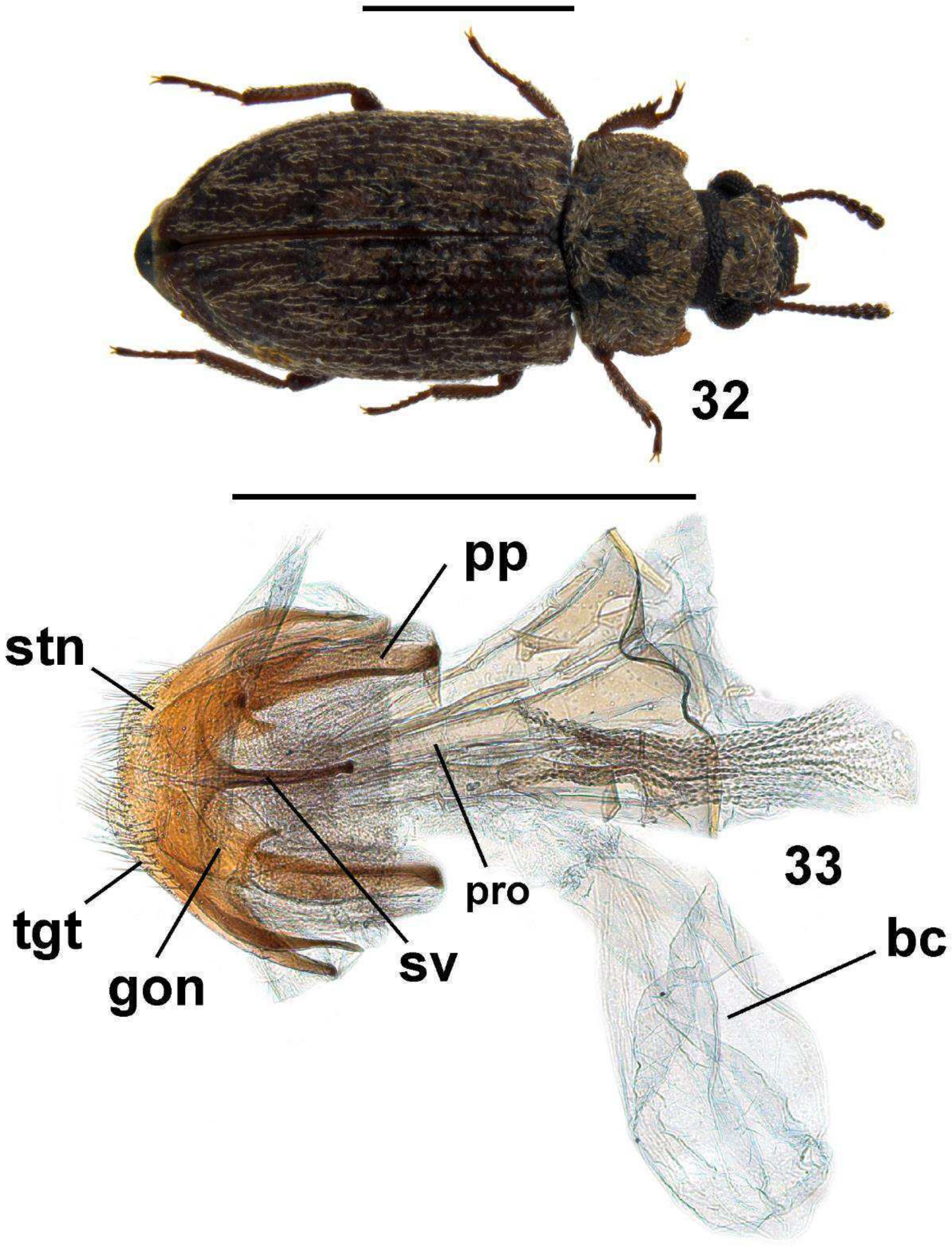
Figures 24-26. *Phaleria testacea*, (24) dorsal view, (25) female abdominal terminalia and (26) ovipositor. **ag** – accessory gland, **gon** – gonocoxite, **gst** – gonostylus, **ip** – inner projection, **pp** – paraproct, **pro** – proctiger, **sp** – spermatheca, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII. Scale bar: 1 mm (Fig. 24) and 0.5 mm (Figs 25–26).



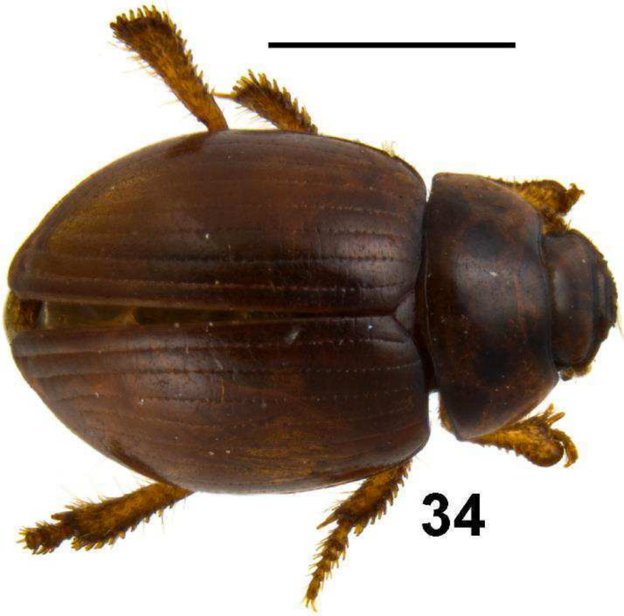
Figures 27–28. *Crypticus quisquilius*, (27) dorsal view and (28) female abdominal terminalia. **bc** – bursa copulatrix, **co** – common oviduct, **gon** – gonocoxite, **gst** – gonostylus, **pp** – paraproct, **pro** – proctiger, **stn** – sternite VIII, **sv** – spiculum ventrale. Scale bar: 1 mm (Fig. 27) and 0.5 mm (Fig. 28).

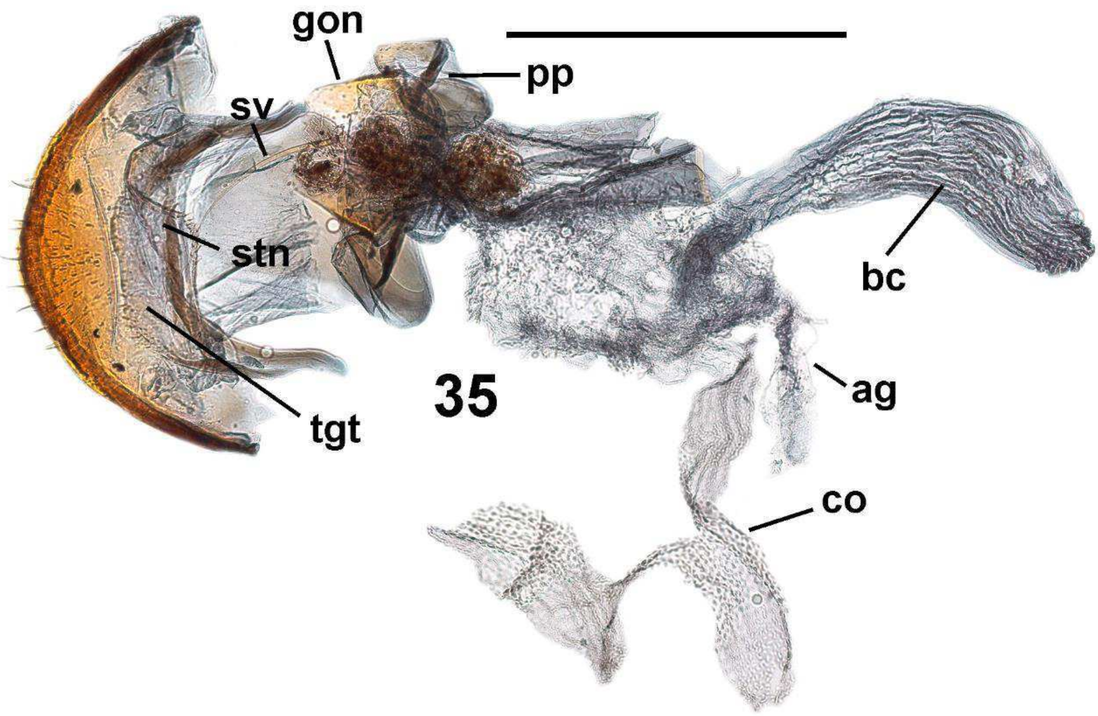


Figures 29–31. *Ectyche tuberculipennis*, (29) dorsal view, (30) female abdominal terminalia and (31) spermatheca. **bc** – bursa copulatrix, **co** – common oviduct, **gon** – gonocoxite, **gst** – gonostylus, **pp** – paraproct, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII, **vs** – vaginal sclerite. Scale bar: 1 mm (Fig. 29), 0.5 mm (Fig. 30) and 0.1 mm (Fig. 31).



Figures 32–33. *Csiro variegata*, (32) dorsal view and (33) female abdominal terminalia. **bc** – bursa copulatrix, **gon** – gonocoxite, **pp** – paraproct, **pro** – proctiger, **stn** – sternite VIII, **sv** – spiculum ventrale, **tgt** – tergite VIII. Scale bar: 1 mm (Fig. 32) and 0.5 mm (Fig. 33).





Figures 34–35. *Trachyscelis pallens*, (34) dorsal view and (35) female abdominal terminalia. **ag** – accessory gland, **bc** – bursa copulatrix, **co** – common oviduct, **pp** – paraproct, **sv** – spicullum ventrale, **stn** – sternite VIII, **tgt** – tergite VIII. Scale bar: 1mm (Fig. 34) and 0.5 mm (Fig. 35).

Table 1. Character matrix of the studied species of Diaperinae. Missing data are represented by question mark (?) and characters not applicable are represented by a n-dash (–).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Alphitophagus bifasciatus	0	0	0	2	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1
Diaperis boleti	0	0	0	0	1	–	1	0	0	2	0	1	0	2	0	0	1	2	1
Menimus ovalis	1	–	–	2	0	0	0	0	0	0	0	1	1	–	–	1	1	1	1
Corticeus unicolor	0	0	1	2	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1
Leiochrinus sauteri	0	1	1	0	0	2	0	2	0	0	1	–	1	–	–	0	1	1	1
Myrmechixenus vaporariorum	?	?	?	1	0	1	0	1	0	0	0	2	?	?	?	?	1	1	1
Scaphidema metallicum	0	1	1	2	0	0	0	0	0	0	0	0	1	–	–	0	1	1	1
Triplehornia metallica	1	–	–	2	0	0	0	0	0	0	0	2	0	2	1	0	1	1	1
Phaleria testacea	0	2	1	2	0	2	2	1	0	1	0	2	?	?	?	0	1	1	1
Crypticus quisquilius	1	–	–	1	0	1	0	0	0	1	0	2	0	1	1	0	1	1	1
Ectyche tuberculipennis	0	2	1	0	0	1	0	0	0	0	0	2	0	1	1	0	0	1	1
Csiro variegata	1	–	–	0	1	–	0	0	1	–	0	2	0	1	1	0	1	2	0
Trachyscelis pallens	1	–	–	0	1	–	0	0	1	–	0	0	0	1	1	0	1	0	1

CAPÍTULO IV – Phylogeny of Diaperinae (Coleoptera: Tenebrionidae) based on morphological characters of adults

(Artigo não publicado. Revista ainda não selecionada)

Phylogeny of Diaperinae (Coleoptera: Tenebrionidae) based on morphological characters of adults

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ABSTRACT

Diaperinae is a quite diverse subfamily with worldwide distribution, and with no clear evidence on the phylogenetic relations of its suprageneric taxa. A comparative study was performed to list characters that could have phylogenetic signals. The analysis includes 15 ingroup species, representing the 11 tribes and the *incertae sedis* genus within the subfamily, as well as 14 outgroups representing the other subfamilies of Tenebrionidae, except for Zolodininae, and a sister family, Ciidae, and 120 morphological characters. Only one tree resulted in the analysis. The only one tribe with more than one representative, Diaperini, was recovered as paraphyletic and Nilioninae appears as part of this tribe. Our results reveal the need to deeply re-evaluate the current classification of the subfamily and relate taxa, but a broader taxon sampling, with more representatives for each tribe and further character exploration, in order to minimize homoplasy even further, is needed in order to fully recognize monophyletic groups and deduce a comprehensive phylogenetic relation between them.

KEY-WORDS: Cladistics; Comparative morphology; Phylogenetic analysis.

INTRODUCTION

Diaperinae is a diverse taxon comprising 11 tribes and one *incertae sedis* genus (Bouchard et al. 2011, Matthews et al. 2010). These beetles are usually found inhabiting humid and tropical forest feeding on basidiomes of fungi (the case of Diaperini and Scaphidemini beetles), on fungi found in the leaf litter or dead trunks (Gnathidiini, Hypophlaeini) or lichens (Leiochrinini, *Triplehornia*), but they can be also found in sand dunes (Phaleriini, Trachyscelini) or other arid and semiarid environments (Ectychini, Hyociini, Crypticini) (Matthews and Bouchard 2008). The taxonomy of the subfamily is quite confused, with many incongruences (Bouchard et al. 2005, 2011, Watt 1974) and almost no easily recognizable characteristic that defines it as monophyletic (Kergoat et al. 2014).

Phylogenetic analyses of Tenebrionidae often encompass a couple of genera (Condamine et al. 2011, Flores and Roig-Juñent 2001, Flores and Vidal 2000, 2009, Kaminski 2013, Palmer 1998) or a single tribe (Bouchard and Yeates 2001, Cifuentes-Ruiz et al. 2014, Flores 2000), rarely reaching the whole family or subfamilies (Doyen 1993, Kergoat et al. 2014). In any case, Diaperinae usually appears with only a few suprageneric taxa analyzed (Kergoat et al. 2014). No phylogenetic analysis, both morphological and molecular, so far have focused on the relations within the subfamily, even with its paraphyly recently appointed (Kergoat et al. 2014). The aim of this paper is to provide insights into a natural classification of Diaperinae and provide a list of characters that may help to access the phylogenetic history of the subfamily.

MATERIAL AND METHODS

Morphological study and terminology

Specimens were examined, measured and dissected under a Zeiss Stemi 2000-C stereomicroscope. In order to facilitate the dissection, the specimens were placed in hot water until softening. After this process, the abdomen was removed and placed in a concentrated KOH solution, under hot bath, until the membranes were softened enough to allow dissection with low damage. Abdominal terminalia were stained with a solution of 0.5% Chlorazol Black E in 85% alcohol to enhance contrast. The extracted parts were kept in plastic vials, immersed in glycerin. Slide preparations were photographed under a Zeiss AxioLab compound microscope equipped with a Zeiss AxioCam MRc digital camera or under a Zeiss Discovery V20 stereomicroscope with a Zeiss AxioCam 506 digital camera, the latter when the parts were too big for the compound microscope. Habitus of adults were photographed under a Zeiss Discovery V20 stereomicroscope with a Zeiss AxioCam 506 digital camera. Final images were the result of montaging image slices at different focal lengths using the extended focus module of Zeiss Axiovision 4.8 software and Zeiss ZEN 2012. The measurements of distances and angles were taken with the proper tool within the Zeiss ZEN 2012 software.

Classification system and taxonomic sampling

The classification of Tenebrionidae follows Bouchard et al. (2011).

The studied specimens belong to the following scientific collections: Australian National Insect Collection (ANIC, Canberra, Australia) and the Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera (CELC, Viçosa, Brazil). A large amount of material was examined, but for the construction of the character matrix a total of 76 specimens of 29 species (Figs 1 – 29) were selected, comprising all suprageneric taxa within Diaperinae, except for Anopidiina (Gnathidiini) and Brittonina and Uptonina (Hyociini) For a better placement of Diaperinae within the family, at least one exemplar species of each other subfamily of Tenebrionidae was included in the outgroup, as well a representative of Ciidae, sister family of Tenebrionidae (Kergoat et al. 2014, Lawrence et al. 2011), for rooting the cladogram. Some outgroup species were chosen *a priori* for representing its inclusive suprageneric taxon, and others were chosen *a posteriori* to have characters represented within both the ingroup and the outgroup, whenever possible. The type genera of the suprageneric taxa studied in both ingroup and outgroup were used when available.

Below is a list of the sampled taxa. Type genera of suprageneric taxa are marked with an asterisk. Label data of specimens are provided in Appendix I.

Outgroup

Tenebrionoidea: Ciidae

**Cis boleti* (Scopoli, 1763) (Fig. 1)

Tenebrionidae: Alleculinae

Lobopoda sp. – Alleculini (Fig. 2)

Tenebrionidae: Lagriinae

Lagria villosa (Fabricius, 1781) – Lagriini (Fig. 4)

Phymatestes sp. – Goniaderini (Fig. 3)

Goniadera sp. – Goniaderini (Fig. 6)

Tenebrionidae: Nilioninae

**Nilio (Linio) lanatus* Germar, 1824 (Fig. 5)

**Nilio (Linio) maculatus* Germar, 1824 (Fig. 7)

Tenebrionidae: Phrenapatinae

Delognatha sp. – Phrenapatini (Fig. 8)

Tenebrionidae: Pimeliinae

Epitragus sp. – Epitragini (Fig. 9)

Lepidocnemeplatia denticulata Triplehorn, 1987 – Cnemeplatini (Fig. 10)

Scotinus sp. – Asidini (Fig 11)

Tenebrionidae: Stenochiinae

Blapida okeni Perty, 1830 – Cnodalonini (Fig. 12)

Tenebrionidae: Tenebrioninae

**Tenebrio molitor* Linnaeus, 1758 – Tenebrionini (Fig. 13)

Trichoton sp. – Opatrini (Fig. 19)

Ingroup: Diaperinae

Crypticini

**Crypticus quisquillius* (Linnaeus, 1760) (Fig. 14)

Diaperini: Diaperina

**Diaperis boleti* (Linnaeus, 1758) (Fig. 20)

Neomida luteonotata (Pic, 1926) (Fig. 16)

Alphitophagus bifasciatus (Say, 1823) (Fig. 15)

Ceropria laticollis Fairmaire, 1903 (Fig. 17)

Ectychini

**Ectyche tuberculipennis* Bates, 1873 (Fig. 24)

Gnathidiini: Gnathidiina

Menimus ovalis (Allard, 1894) (Fig. 25)

Hyociini: Hyociina

Csiro variegata (Blackburn, 1894) (Fig. 18)

Hypophlaeini

**Corticeus unicolor* (Piller and Mitterpacher, 1783) (Fig. 26)

Leiochrinini

**Leiochrinus sauteri* Kaszab, 1946 (Fig. 27)

Myrmechixenini

**Myrmechixenus vaporariorum* Guérin-Méneville, 1843 (Fig. 21)

Phaleriini

**Phaleria testacea* Say, 1824 (Fig. 22)

Scaphidemini

**Scaphidema metallica* (Fabricius, 1792) (Fig. 23)

Trachyscelini

**Trachyscelis pallens* Champion, 1893 (Fig. 28)

Incertae sedis

Triplehornia metallica Matthews and Lawrence, 2005 (Fig. 29)

Terminology and definition of characters

The morphological nomenclature follows Doyen and Tschinkel (1982) and Matthews et al. (2010). The format of character statements follows Sereno (2007). The characters were defined by direct observation of specimens and dissected parts in search for traits variable between species. Part of the characters used here was based or modified from previously published phylogenetic works on Coleoptera (Lawrence et al. 2005, 2011). Character states based on ratios were defined *a posteriori*, after evaluating non-overlapping variation ranges acceptable both mathematically and biologically. From now on in the text, each character is abbreviated as "C" followed by the respective character number, and states as "S" followed by the state number (so, for the character 1, state 0, the quotation will be C2-S0).

Cladistic analysis

The data matrix was compiled using the software Mesquite (Maddison and Maddison 2019). Characters were defined following Serrano (2007). In the cases when the character was not observable it was coded as '?', and those inapplicable were coded '-'. We coded 92 out of the 123 characters as binary, and the multi-state characters were treated as unordered. Heuristic searches were performed under equal weights (EW) and implied weights (IW) (Goloboff 1993, Goloboff *et al.* 2008) using the TnT (Goloboff et al. 2003b) Traditional search algorithms, both performed with 70000 replicates, saving 50 trees per replication. In the IW run the k-value used was 6.106, following the protocol proposed by Mirande (2009) for the fittest k-value.

For EW analysis, the Bremmer support (Bremer 1994) was calculated following Davoto (2015). The IW analysis was evaluated by symmetric resampling (Goloboff et al. 2003a), Bootstrap (Efron 1979) and Jackknife (Quenouille 1949), using 10000 replicates each and default parameters.

RESULTS

List of characters

A total of 123 characters were defined, of which three were non-informative since all taxa analyzed had the same state for each character (marked with asterisk). All characters led to 3480 possible entries in the matrix (excluding non-informative entries), of which 201 were marked as unknown (?) and 179 as inapplicable (-). The list of characters is provided below.

Head

1. *Head, dorsal, if covered by pronotal projection: not covered (0); covered (1). (modified from Lawrence et al. 2011).
2. Head, orientation: prognathous (0); hypognathous (1).
3. Head, width relative to its length: longer than wide (0); as wide as long (1); wider than long (2). (Figs 30 – 31)

   The measurement for length is made from the anterior limit of the clypeus to the posterior limit of the occipital region. When the clypeus is notched at the middle, the limit anteriorly is taken by an imaginary line between the two clypeal lobes. The width is taken in the widest point of head, excluding the eyes.
4. Postoccipital edge of head, whether emarginate or not: emarginate (0); not emarginate (1). (modified from Lawrence et al. 2011). (Fig. 30)

   Here, the emarginations, when present, can be observed with the head in dorsal view. The post occipital edge is considered emarginate when the occipital foramen has one or two indentations posteriorly, that surpasses the imaginary strait line connecting the other points of the foramen.
5. Postoccipital edge of head, number of emarginations: 1 (0); 2 (1).

   Inapplicable when C4 = S1. (modified from Lawrence et al. 2011).
6. Clypeus, whether conspicuously separate from frons or not: conspicuously separate (0); not conspicuously separate (1). (Fig. 30)

   The separation, when conspicuously visible, can be presented as a suture that separates the clypeus and the frons, without forming an articulation, or it can be freely articulated with frons.
7. Clypeus, width relative to its length: less than twice wider (0); two to four times wider than long (1); four or more times wider than long (2). (Fig. 30)
8. *Eyes, whether present or not: present (0); absent (1).
9. Eyes, dorsal, ratio of the shortest distance between eyes and the greatest width of head: less than half the width of head (0); more than half the width of head (1).

   Inapplicable when C8 = S1. (Fig. 30)
10. Eyes, ventral, ratio of the shortest distance between eyes and the greatest width of head: less than half the width of head (0); more than half the width of head (1).

    Inapplicable when C8 = S1.
11. Eyes, dorsal, ratio of the length of the left eye and the length of head: less than 1/3 the length of head (0); more than 1/3 the length of head (1).

Inapplicable when C8 = S1.

12. Eyes, lower lobe of left eye, whether shorter or longer than the upper lobe: smaller (0); longer (1).

    Inapplicable when C8 = S1.

13. Eyes, whether emarginate by genal margins or not: emarginate (0); not emarginate (1). (modified from Lawrence et al. 2011). (Fig. 31)

    Inapplicable when C8 = S1.

14. Eyes, anteromedial emargination, whether weakly or strongly emarginate: weakly (0); strongly (1). (modified from Lawrence et al. 2011).

    Was considered as weakly emarginate those eyes in which the emargination does not break the rounded shape of eye in lateral view, and strongly emarginate when the eye becomes somewhat reniform in lateral view. Inapplicable when C8 = S1 or C13 = 1.

15. Labrum, width relative to its length: less than twice wider (0); two or more times wider (1). (Fig. 32)
16. Labrum, apex, shape: rounded (0); truncate (1); bilobed (2). (modified from Lawrence et al. 2011). (Fig. 32)
17. Torma, medial process, whether present or not: present (0); absent (1).
18. Torma, medial process, length relative to length of labrum: less than half the length of labrum (0); more than half the length to as long as length of labrum (1); longer than labrum (2). (Fig. 32)

    Inapplicable when C17 = S1.

19. Torma, posterior process, whether present or not: present (0); absent (1).
20. Torma, posterior process, length relative to length of labrum: less than half the length of labrum (0); more than half the length to as long as length of labrum (1); longer than labrum (2). (Fig. 32)

    Inapplicable when C19 = S1.

21. Antenna, left, scape, length relative to length of pedicel: less than twice the length of pedicel (0); two or more times longer than pedicel (1). (modified from Lawrence 2011). (Fig. 37)
22. Antennae, modifications starting at segment: 3 or less (0); 4 (1); 5 or more (2). (modified from Lawrence et al. 1995). (Fig. 37)

    Usually the modification found is the enlargement of the segments, but it was also considered changes in shapes for this character. State 0 comprises the antennae with the modifications starting in the first segment after pedicel or before, which means it is virtually without any conspicuous modifications.

23. Antennae, stellate sensoria, whether present or not: present (0); absent (1). (Fig. 37)
    Stellate sensoria can also be called multipronged sensilla. It is a rounded patch of sensilla, usually lighter colored than the segment and with somewhat a star shape in larger magnifications.
24. Antennae, stellate sensoria, position on the segments: at the apex of the segment (0); in all surface of the segment (1).
    Inapplicable when C23 = S1.
25. Antenna, left, stellate sensoria, number per segment: less than 10 (0); 10 or more (1).
    Inapplicable when C23 = S1.
26. Antenna, left, stellate sensoria, size relative to width of preapical segment: less than 1/10 the width of segment (0); more than 1/10 but less than 1/5 the width of segment (1); more than 1/5 the width of segment (2). (Fig. 37)
    The ratio was made with the mean diameter of, at least, three antennomers of the same segment with the width measured, in this case, the preapical segment. Inapplicable when C23 = S1.
27. Antennae, whether apical segments enlarge to forming a club or not: segments enlarging to form a club (0); segments not enlarging to form a club (1). (Fig. 37)
28. Antenna, left, club, number of segments: 4 or less (0); 5 or more (1).
    Inapplicable when C27 = S1.
29. Mandible, left, width relative to its length: longer than wide (0); as wide as or wider (1). (modified from Lawrence et al. 2011). (Fig. 33)
    The width is measured in the widest point of the mandible, in ventral or dorsal view.
30. Mandible, left, internal width relative to its length: less than half the length (0); more than half the length (1). (Fig. 34)
    The width is measured in the widest point of the mandible, excluding the mola and condyles. This point is usually right in front of the molar region. The positioning of the mandible for this measurement is in lateral view, with the mola or molar region facing upwards.
31. Mandibles, prostheca, whether present or not: present (0); absent (1). (modified from Lawrence et al. 2011). (Fig. 33)
32. Mandibles, mola, whether present or not: present (0); absent (1). (modified from Lawrence et al. 2011). (Fig. 33)

33. Mandible, left, mola, length relative to its width: wider than long (0); as wide as long but less than twice the width (1); more than twice the width (2). (Fig. 33)
    Inapplicable when C32 = S1.
34. Mandible, left, mola, length relative to length of mandible: 1/3 or less the length of mandible (0); more than 1/3 the length of mandible (1).
    Inapplicable when C32 = S1.
35. Mandible, left, mola, whether striate or not: striate (0); not striate (1). (Fig. 34)
    Inapplicable when C32 = S1.
36. Mandible, left, apical teeth, number: 1 (0); 2 (1); 3 (2). (Fig. 33)
37. Maxillae, apical palpomere, shape: subcylindrical (0); subtriangular (1). (modified from Lawrence et al. 2011). (Fig. 35)
    Subcylindrical is considered the shape in which the sides are somewhat parallel or slightly converging in a fusiform shape. In the subtriangular shape, the apex is oblique.
38. Maxilla, left, mediostipes, width relative to its length: longer than wide (0); as long as wide or wider (1). (Fig. 35)
39. Maxilla, left, lacinia, uncus, whether present or not: present (0), absent (1). (modified from Lawrence et al. 2011). (Fig. 35)
40. Ligula, length relative to length of mentum: shorter (0); as long as or longer (1). (Fig. 36)
41. Mentum, shape: subquadrate (0); trapezoidal (1). (Fig. 36)
    Subquadrate is presented as the four sides somewhat parallel. In the trapezoidal shape, two sides are parallel and two sides are in angle two each other.
42. Gula, area between gular sutures, width relative to its length: longer than wide (0); as long as or wider (1). (modified from Lawrence et al. 2011). (Fig. 31)

Prothorax

43. Prothorax, width relative to its length: longer than wide (0); wider than long (1). (Fig. 38)
44. Prosternum, length relative to length of prosternal process: less than half the length of prosternal process (0); more than half but then the length of prosternal process (1); longer than prosternal process (2). (Fig. 38)

45. Prosternum, width relative to its length: three times wider or less (0); three to five times wider (1); five or more times wider (2). (Fig. 38)
46. Prosternal apophysis, length relative to length of left procoxal cavity: less than half the length of procoxal cavity (1); more than half but less than the length of procoxal cavity (1); longer than procoxal cavity (2). (modified from Lawrence et al. 2011). (Fig. 39)

    The term prosternal apophysis refers to the internal invagination found in the prothorax. This follows the nomenclature used by Doyen (1966). It can be found also called by “proendosternite” (Doyen 1966; Flores 2000).
47. Prosternal apophysis, apex, shape: acute (0); widened (1). (Fig. 39)

Pterothorax

48. Mesonotum, whether freely articulated with elytra or not: freely articulated (0); not freely articulated (1). (Fig. 40)
49. Mesonotum, width relative to its length: longer than wide (0); as long as to two times wider (1); more than two times wider (2). (Fig. 40)
50. Mesonotum, length of mesoscutum relative to length of mesoscutelum: less than twice the length of mesoscutelum (0); two to three times the length of mesoscutelum (1); more than three times the length of mesoscutelum (2).
51. Mesonotum, longitudinal mesothoracic suture, whether present or not: present (0); absent (1). (Fig. 40)
52. Mesonotum, longitudinal mesothoracic suture, length relative to length of mesoscutum: less than half the length of mesoscutum (0); more than half the length of mesoscutum (1).

    Inapplicable when C51 = S1.
53. Mesonotum, mesoscutelum, width relative to its length: longer than wide (0); as long as to two times wider (1); two or more times wider than long (2).
54. Mesonotum, yolk plate, whether present or not: present (0); absent (1).
55. Mesonotum, yolk plate, whether laterally longer or shorter than mesonotum: longer (0); shorter (1). (Fig. 40)

    This character is visualized by drawing an imaginary sagittal line in the leftmost point of the mesonotum, if the yolk plate passes laterally this line, then the state 0 is given.

    Inapplicable when C54 = S1.

56. Mesonotum, yolk plate, width relative to its length: less than 1/3 the length (0); more than 1/3 the length (1).
    Inapplicable when C54 = S1.
57. Metanotum, width relative to its length: less than twice the length (0); two or more times wider (1). (Fig. 41)
58. Metanotum, antecostal suture, width relative to width of metanotum: half the width of metanotum or less (0); more than half the width of metanotum (1). (Fig. 41)
59. Metanotum, scutellar groove, length relative to its width: less than twice the width (0); two to four times the width (1); four times the width or more (2). (Fig. 41)
60. Metanotum, alar ridge of metascutelum, whether parallel or converging posteriorly: parallel (0); converging posteriorly (1). (Fig. 41)
61. Mesoventrite, length relative to length of metaventrite: less than the length of metaventrite (0); as long as but less than twice the length of metaventrite (1); twice the length of metaventrite or more (2). (Fig. 42)
62. Mesoventrite, length relative to its width: less than half the width (0); more than half the width (1). (Fig. 42)
63. Metaventrite, length relative to its width: less than half the width (0); more than half the width (1). (Fig. 42)
64. Metaventrite, discrimen, whether present or not: present (0); absent (1). (modified from Lawrence et al. 2011). (Fig. 42)
65. Metaventrite, discrimen, length relative to length of metaventrite: less than half the length of metaventrite (0); more than half the length of metaventrite (1). (Fig. 42)
    Inapplicable when C64 = S1. (modified from Lawrence et al. 2011).
66. Metendosternite, laminae, aperture angle: less than 90º (0); 90º or more (1). (Fig. 43)
    The angle is measured from the divergency point of both laminae to its points in a straight line.
67. Metendosternite, stalk, length relative to length of laminae: less than half the length of laminae (0); more than half the length of laminae (1). (Fig. 43)
68. Metacatepisternal suture, whether present or not: present (0); absent (1). (modified from Lawrence et al. 2011). (Fig. 42)
69. Metacatepisternal suture, extension: less than halfway to lateral of metaventrite (0); more than halfway to almost reaching the lateral of metaventrite (1).
    Inapplicable when C68 = S1. (modified from Lawrence et al. 2011).
70. Hind wings, whether present or not: present (0); absent (1).

71. Hind wings, length relative to length of body: less than half the length of body (0); more than half but less than the length of body (1); more than the length of the body (2).
    Inapplicable when C70 = S1.
72. Hind wings, medial field, venation, whether present or not: present (0); absent (1). (Fig. 44)
    Inapplicable when C70 = S1.
73. Hind wings, apical field, venation, whether present or not: present (0); absent (1). (Fig. 44)
    Inapplicable when C70 = S1. (modified from Lawrence et al. 2011).
74. Hind wings, radial cell, whether present or not: present (0); absent (1). (Fig. 44)
    Inapplicable when C70 = S1. (modified from Lawrence et al. 2011).
75. Elytra, median suture, degree of closure: loosely closed (0); strongly closed or fused (1). (Fig. 45)
    The state 1 is easily observable in the specimens with fused elytra. In the case of elytra not completely fused, the state can be observed by being hardly than usual to open, and by observing parts of the suture ripped off as a result of opening the elytra (Fig. 45, els)
76. *Elytra, epipleura, whether present or not: present (0); absent (1).
77. Elytra, epipleura, whether extending to apex of elytra or not: extending to apex of elytra (0); not extending to apex of elytra (1). (Fig. 45)
    Inapplicable when C76 = S1. (modified from Lawrence et al. 2011).

Legs

78. Preapical tarsomere, mesotarsus, whether lobed or not: lobed (0); not lobed (1). (Fig. 47)
79. Tibiae, mesotibiae, apical inner angle, whether present or not: present (0); absent (1). (Fig. 47)
80. Tibiae, mesotibiae, apical inner angle, number of teeth: 1 (0); 2 (1).
    Inapplicable when C79 = S1.
81. Procoxa, left, length relative to length of left profemur: less than half the length of profemur (0); more than half the length but less than the length of profemur (1); longer than profemur (2). (Fig. 46)

To measure the length of procoxae, the entire coxa needs to be removed unarmed from the coxal cavity.

82. Procoxae, distance between procoxae in relation to width of left procoxa: less than half the width of procoxa (0); more than half the width but less than the width of procoxa (1); wider than procoxa (2). (Fig. 38)
83. Procoxae, degree of enclosure posteriorly: closed (0); weakly closed (1); open (2). (Fig. 38)

    Closed refers to the coxae that is closed by a plate larger than half the length of coxa, and weakly closed, by a plate shorter than half the length of coxa.
84. Protibia, left, outer apical angle, whether expanded or not: expanded (0); not expanded (1). (Fig. 46)

    The expansion is considered when abrupt, those tibiae with gradual expansion towards apex, were considered as not expanded.
85. Mesocoxae, whether separate or contiguous: separate (0); contiguous (1). (modified from Lawrence et al. 2011).
86. Mesocoxae, distance between mesocoxae in relation to width of left mesocoxa: less than half the width of mesocoxa (0); more than half the width but less than the width of mesocoxa (1); wider than mesocoxa (2). (modified from Lawrence et al. 2011). (Fig. 42)

    Inapplicable when C85 = S1.
87. Mesocoxae, whether closed by mesepimeron or mesoventrite: closed by mesepimeron (0); closed by mesoventrite (1). (modified from Lawrence et al. 1995). (Fig. 42)

    The coxa, when closed by mesepimeron, is also surrounded by mesoventrite, in the case of state 1, the only two plates in contact with the coxal cavity are the meso and metaventrites.
88. Metacoxae, distance between metacoxae in relation to width of left metacoxa: less than half the width of metacoxa (0); more than half the width but less than the width of metacoxa (1); wider than metacoxa (2). (Fig. 42)

Abdomen

89. Abdomen, length relative to its width: wider than long (0); as long as wide or longer (1). (Fig. 48)

90. Abdomen, abdominal process, shape: acute (0); rounded or truncate (1). (Fig. 48)
91. Abdomen, abdominal ventrite 1, shortest length in relation to its longest length: less than half the length (0); more than half the length but less than as long as (1); longer (2). (Fig. 48)
92. Abdomen, membrane between apical ventrites, whether visible or not: visible (0); not visible (1).

    To this character, the abdomen is observed in rest position.

Male abdominal terminalia

93. Aedeagus, length relative to length of exposed abdomen: less than half the length of abdomen (0); more than half the length but less than the length of abdomen (1); longer than abdomen (2).
94. Aedeagus, parameres, whether fused or not: fused (0); not fused (1).
95. Aedeagus, parameres, degree of fusion: completely fused (0); partially fused (1). (Fig. 49)

    Inapplicable when C94 = S1.
96. Aedeagus, parameres, length relative to length of basal piece: less than half the length of basal piece (0); more than half the length but less than the length of basal piece (1); longer than basal piece (2).
97. Aedeagus, parameres, alae, whether present or not: present (0); absente (1).

    Alae refers to the portion of parameres that surpasses, in the direction of the basal piece, the point of articulation with the basal piece.
98. Aedegaus, penis, length relative to length of basal piece: present (0); absent (1).
99. Spiculum gastrale, whether present or not: present (0); absent (1).
100. Spiculum gastrale, lateral arms, whether fused or not: fused (0); not fused (1).

     Inapplicable when C99 = S1.
101. Spiculum gastrale, lateral arms, degree of fusion: completely fused from base (0); fused from basal half (1); fused after basal half (2). (Fig. 50)

     Inapplicable when C99 = S1 or C100 = S1.

Female abdominal terminalia[1]

102. Spermatheca, whether present or not: present (0); absent (1).

103. Spermatheca, shape: rounded (0); reniform (1); tubular (2). (Figs 53 – 55)
Here the spermathecal shape found in *Nilio* (Fig. 54) is considered to be a rounded shape with constriction, placing this shape as closely related to those within Diaperini (Fig. 53), following Tschinkel and Doyen (1980). Inapplicable when C102 = S1.
104. Spermatheca, invaginations, whether present or not: present (0); absent (1). (Figs 53 – 54)
105. Gonocoxites, length relative to its width: wider than long (0); as long as wide (1); longer than wide (2).
106. Gonocoxites, ventral lobes, whether visible or not: visible (0); not visible (1).
107. Gonocoxites, ventral lobes, number: 4 (0); 3 (1); 2 (2).
Inapplicable when C106 = S1.
108. Gonocoxites, modifications at apex, whether present or not: present (0); absent (1).
109. Gonocoxites, modifications at apex, shape: teeth (0); long, narrow projection (1).
Inapplicable when C108 = S1. (Figs. 51 – 52)
110. Gonocoxites, baculi, whether present or not: present (0); absent (1).
111. Gonocoxites, baculi, orientation relative to gonocoxites: oblique (0); transverse (1).
Inapplicable when C110 = S1.
112. Gonostyli, whether present or not: present (0); absent (1).
113. Gonostyli, insertion relative to apical lobe of gonocoxites: apical (0); lateral (1); dorso-lateral (2). (Figs 51 – 52)
Inapplicable when C112 = S1.
114. Spiculum ventrale, whether present or not: present (0); absent (1).
115. Spiculum ventrale, length relative to length of ovipositor: shorter (0); longer (1).
Inapplicable when C114 = S1.
116. Bursa copulatrix, whether present or not: present (0); absent (1).
117. Bursa copulatrix, length relative to length of ovipositor: shorter (0); longer (1).
Inapplicable when C116 = S1.
118. Bursa copulatrix, modifications, whether present or not: present (0); absent (1).

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[1] These characters were modified from the qualification paper presented in Chapter III of this thesis. Modifications were made in the characters 7 and 8 (here called 108–109 and 110–111, respectively) in order that neomorphic and transformational characters appeared separately.

Inapplicable when C116 = S1.

119. Bursa copulatrix, modifications, type: window (0); sclerite (1). (Figs 56 – 57) Inapplicable when C116 = S1 or C118 = S1.
120. Accessory gland, whether bifurcate or not: bifurcate (0); not bifurcate (1).
121. Vagina, sclerites, whether present or not: present (0); absent (1).
122. Paraprocts, length relative to length of ovipositor: shorter (0); as long as (1); longer (2).
123. Paraprocts, baculi, orientation relative to ovipositor: parallel (0); oblique (1).

Phylogenetic analysis

The heuristic search of characters with EW resulted in 29 most parsimonious trees of 557 steps, with CI=0.27 and RI=0.40. The strict consensus tree with Bremer support values is shown in Figure 58. Only two nodes received high nodal support value (>50). Diaperinae was recovered as polyphyletic, although the nodes were not collapsed, but it was maintained with very low support (>10). Only *Nilio* spp. and Tenebrionidae was recovered as monophyletic with a support value of 100. The Lagriinae, Goniaderini and Scaphidemini + Leiochrinini clades were recovered as monophyletic with low nodal supports of 20, 33 and 20, respectively.

The IW analysis resulted in a single most parsimonious tree (Fig. 59). The strict consensus trees are shown with Symmetric Resampling (SR, Fig. 60), Bootstrap (BS, Fig. 61) and Jackknife frequencies (JK, Fig. 62). The results were quite similar with those of EW analysis, with only Tenebrionidae (SR=100, BS=100, JK=100) and *Nilio* (SR=99, BS=98, JK=99) clades supported, differing from Diaperinae nodes collapsed, and a higher support value for the Lagriinae (SR=45, BS=23, JK=51), Goniaderini (SR=35, BS=28, JK=38) and Scaphidemini + Leiochrinini (SR=45, BS=26, JK=52). The Jackknife analysis also shown as marginally supported the clades *Triplehornia* + Ecthychini + Asidini + Gnathidiini (JK=46) and Ecthychini + Asidini + Gnathidiini (JK=45). Those clades were also recovered in Symmetric Resampling and Bootstrap as monophyletic, but with lower support values.

DISCUSSION

This was the first attempt to reconstruct the phylogenetic history of Diaperinae using morphological characters and analyzing a broad number of the suprageneric taxa. Our findings are similar to those recovered by Kergoat et al. (2014) using molecular data, on evidencing a non-monophyletic relationship between Diaperinae suprageneric taxa.

The EW analysis (Fig. 58) showed Diaperinae as a para/polyphyletic taxon, with *Csiro variegata* excluded from the main clade and with Stenochiinae and Lagriinae within the Diaperinae clade. However, these clades are unsupported with Bremer support values calculated just barely above 0, with the highest being 33 in the Goniaderini clade. The only supported clades are the Tenebrionidae and Nilioninae, the later with only two species from the same subgenus sampled.

The IW analysis showed similar results, only emphasizing the paraphyletic nature of Diaperinae. The analysis with Symmetric Resampling (Fig. 59) the same Tenebrionidae and Nilioninae clades appeared as the only supported ones, but some as the Lagriinae and Scaphidemini + Leiochrinini clades appeared with marginal support with values of 43 and 45 respectively. The Bootstrap analysis (Fig. 60) also only supported the Tenebrionidae and Nilioninae clades. The Jackknife analysis (Fig. 61) also supported Tenebrionidae and Nilioninae clades, but also supported the Lagriinae and Scaphidemini + Leiochrinini clades, marginally supported in the SR analysis, and marginally supported the *Triplehornia* + Ectychini + Asidini + Gnathidiini clade, with support value of 46.

The relation of *Triplehornia metallica* could not be accessed with our analysis (SR=37, BS= 22, JK= 46), possibly due to the small number of characters accessed, since we did not have specimens that we could completely dissect. The genus shares characters with many Diaperinae tribes, such as the not complete epipleura, reduced wing venation and metendosternite structure shared with Leiochrinini and Gnathidiini; and the aedeagal alae shared with Scaphidemini and Leiochrinini (Matthews and Bouchard 2008). Its positioning and phylogenetic relations could possibly be accessed with a more detailed analysis of the characters and the search for new ones to include in the matrix.

Leiochrinini and Scaphidemini returned as a clade (JK=52), corroborating the relations of these two tribes as mentioned by Matthews and Bouchard (2008). They mentioned that the similarities of those two tribes falls to the internally open procoxal cavities, smooth molar surfaces, no corpotentorium and T-shaped spermatheca. Here, we found that what placed these two tribes in the same clade was the not emarginated postoccipital edge of head (C4-S1); the length of the wings longer than the length of the body (C71-S2); the metacoxae separated by more than a half but less than the length of the left metacoxal (C88-C1); the spermatheca reniform (C103-S1), which was an apomorphie for this clade and the shape, even with different name, is the same shape cited by Matthews and Bouchard (2008); and the absence of a bursa copulatrix (C116-S1).

Diaperinae is informally treated as possessing two different lineages or branches, the “phaleriine” Diaperinae and the “diaperine” Diaperinae (Matthews and Bouchard 2008). The first consisting those tribes with relations to xeric and sand environments, namely Phaleriini, Hyociini, Crypticini, Ectychini and Trachyscelini, and the later, those who live in mesic and humid forests, namely Diaperini, Hypophlaeini, Leiochrinini, Scaphidemini, Myrmechixenini and Gnathidiini. In our analysis, these lineages were not recovered. The “diaperine” branch returned partially related (Fig. 62), but with low support. Since it was almost one single tribe that held this branch and Phaleriini appeared as related to it, these two lineages are probably held by homoplasic characters, as most of those characters are associated to the habitat in which the species are found, therefore, derived from convergent evolution.

The number of homoplasies recovered in the final IW tree (Fig. 63) possibly lead to the low support of the clades returned in the analysis. Some of the characters recovered as homologies are, in fact, homoplasies due to convergent evolution, such as the absence of hind wings (C70-S1) and the fused elytra (S75-S1), which supports the Ectychini + Asidini + Gnathidiini clade, which cover soil inhabiting species of xeric environment.

CONCLUSION

Both EW and IW analysis refutes the monophyletic nature of Diaperinae and recovers the clade Scaphidemini + Leiochrinini, already discussed in the literature as possibly related.

The general low support values found in all analysis, evidence the difficulties of find phylogenetically responsive characters for Diaperinae and the need of a more detailed morphological study in order to find new and possibly non-orthodoxical characters, which may help to elucidate the phylogenetic history of the subfamily.

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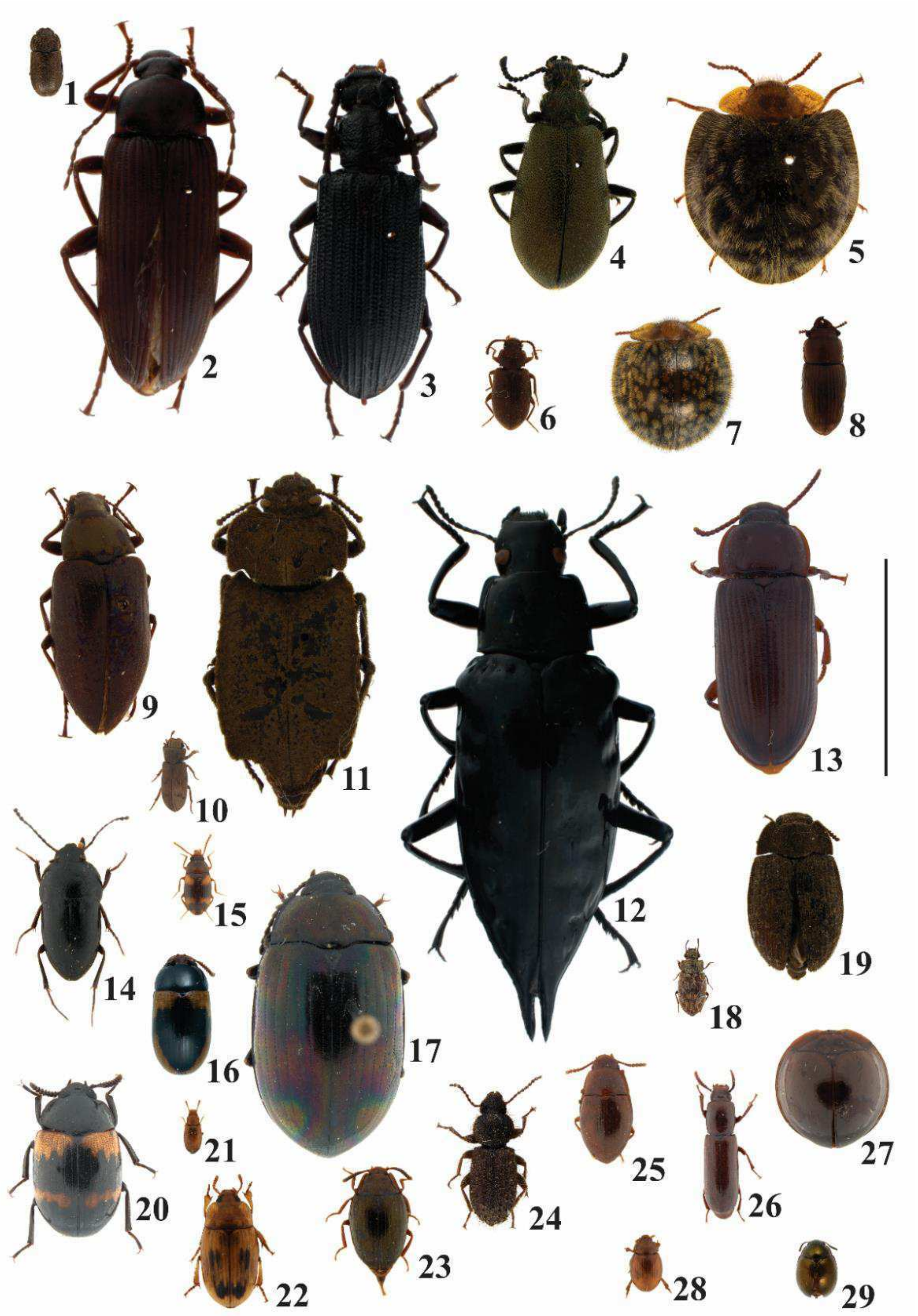
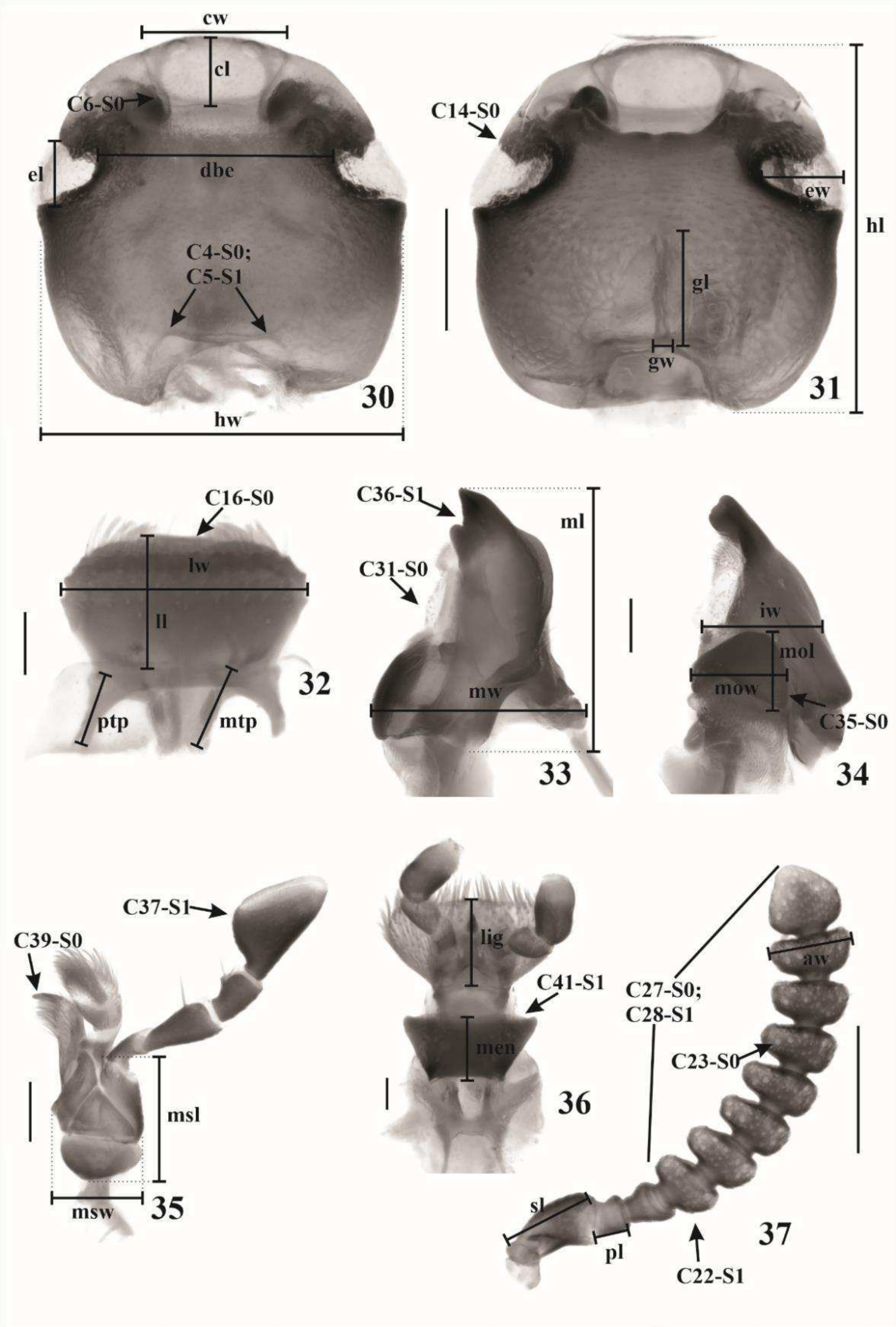
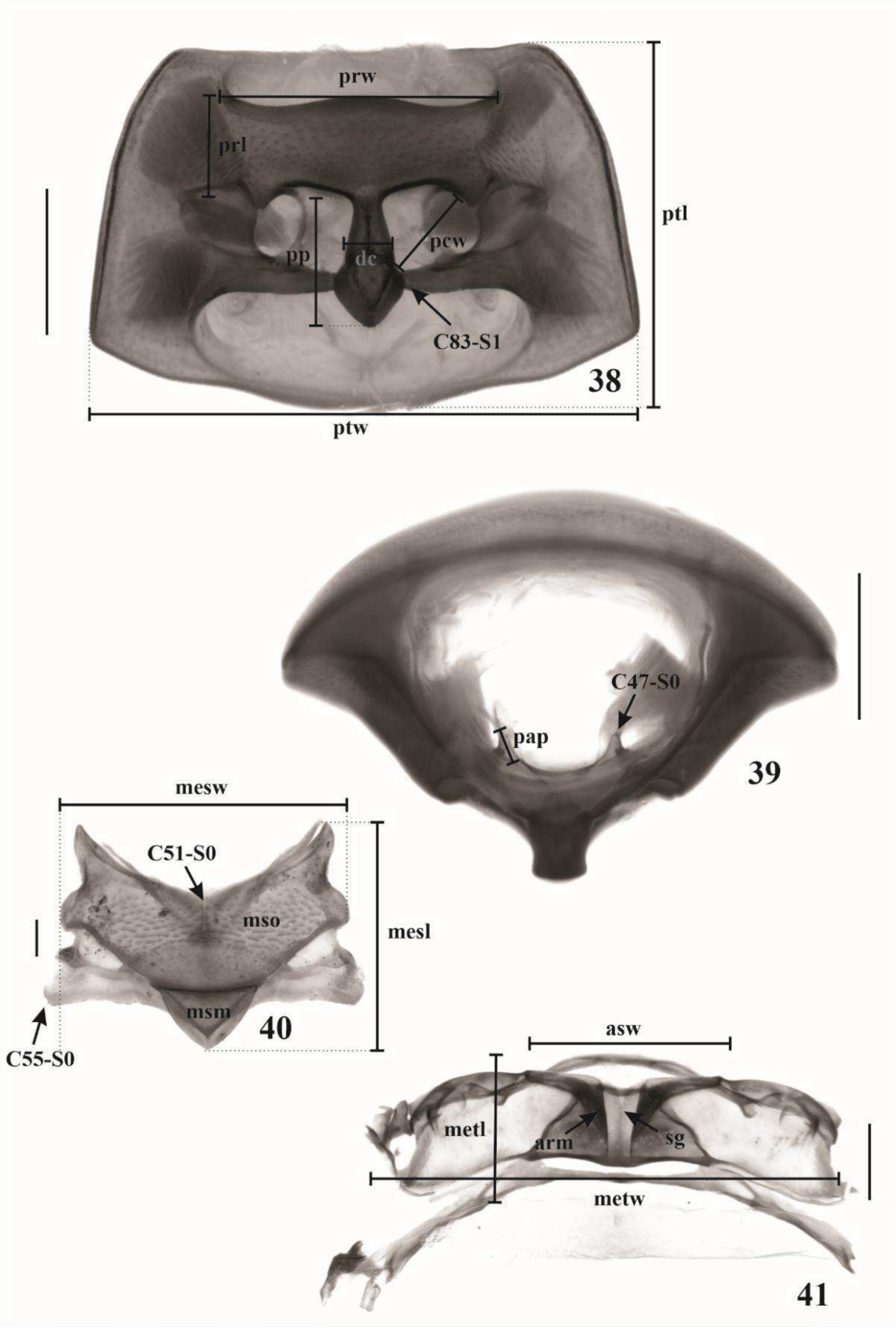


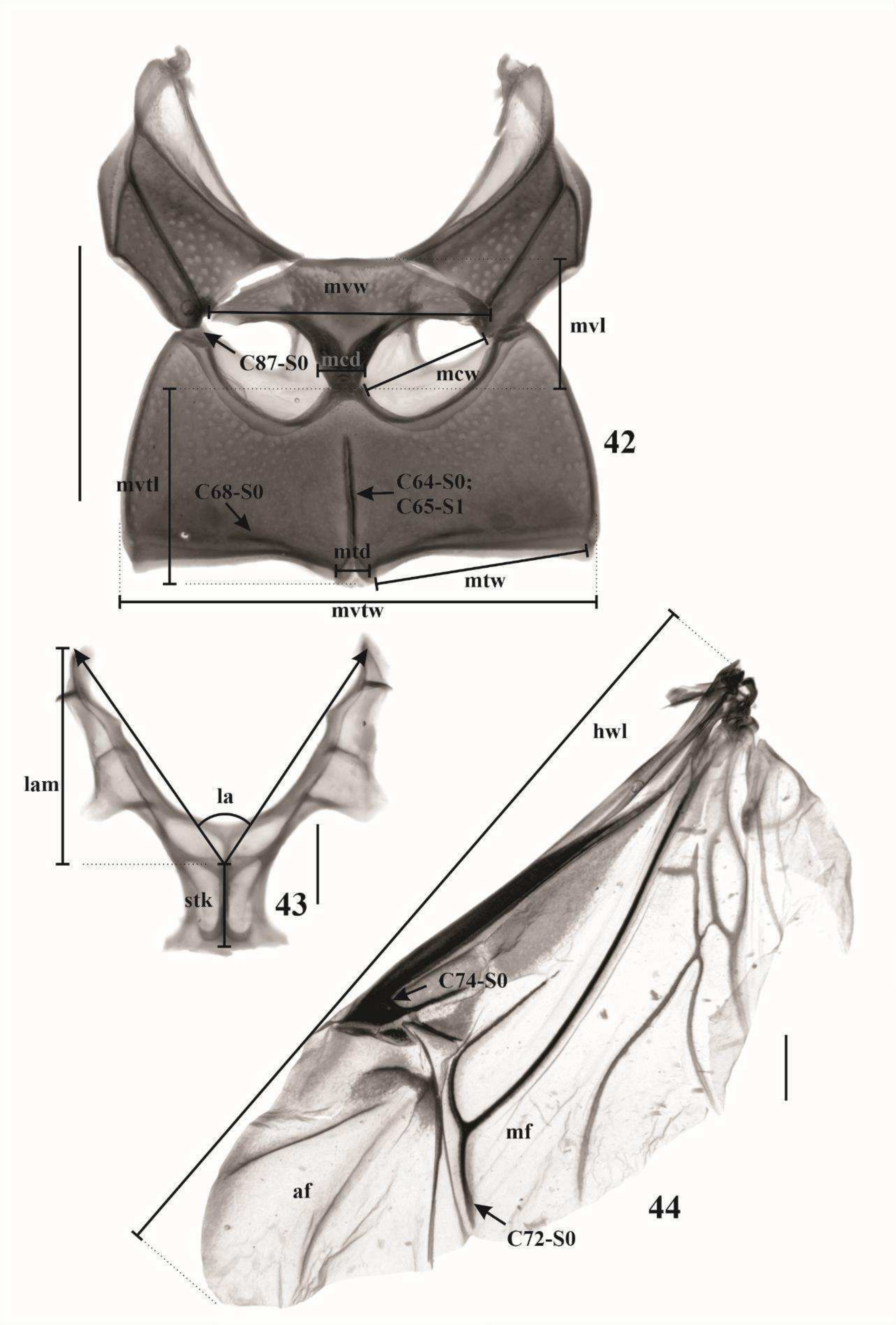
Figures 1 – 29. Habitus of the species studied. 1, *Cis* boleti (Scopoli, 1763); 2, *Lobopoda* sp.; 3, *Phymatestes* sp.; 4, *Lagria villosa* (Fabricius, 1781); 5, *Nilio (Linio) lanatus* Mader, 1936; 6, *Goniadera* sp.; 7, *Nilio (Linio) maculatus* Mader, 1936; 8, *Delognatha* sp.; 9, *Epitragus* sp.; 10, *Lepidocnemeplatia denticulata* Triplehorn, 1987; 11, *Scotinus* sp.; 12, *Blapida okeni* Perty, 1930; 13, *Tenebrio molitor* Linnaeus, 1758; 14, *Crypticus quiaquillius* (Linnaeus, 1760); 15, *Alphitophagus bifasciatus* (Say, 1823), 16, *Neomida luteonotata* (Pic, 1926), 17, *Ceropria laticollis* Fairmaire, 1903; 18, *Csiro variegata* (Blackburn, 1894); 19, *Trichoton* sp.; 20, *Diaperis boleti* (Linnaeus, 1758); 21, *Myrmechixenus vaporariorum* Guérin-Méneville, 1843; 22, *Phaleria testacea* Say, 1824; 23, *Scaphidema metallica* (Fabricius, 1792); 24, *Ecthyche tuberculipennis* Bates, 1873; 25, *Menimus ovalis* (Allard, 1894); 26, *Corticeus unicolor* (Piller and Mitterpacher, 1783); 27, *Leiochrinus sauteri* Kaszab, 1946; 28, *Trachyscelis pallens* Champion, 1893; 29, *Triplehornia metallica* Matthews and Lawrence, 2005. Scale bar = 1 cm.



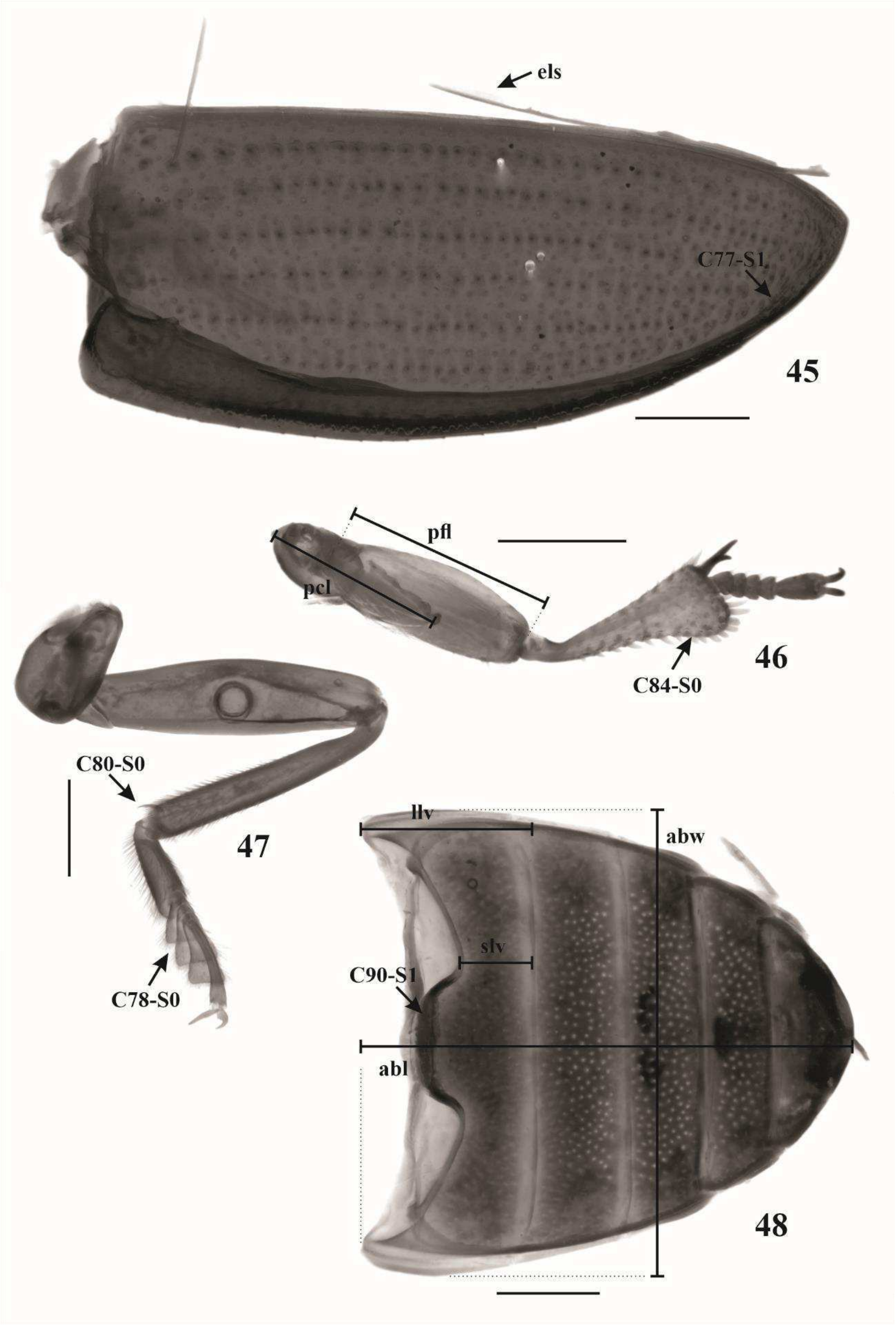
Figures 30 – 37. Head, *Neomida luteonotata*, 30, dorsal; 31, ventral. Labrum, *Csiro variegata*, 32, dorsal. Left mandible, *Ceropria laticollis*, 33, ventral; 34, inner view. Left maxilla, *Crypticus quisquillius*, 35, ventral. Labrum and mentum, *Ceropria laticollis*, 36, ventral. Left antenna, *Diaperis boleti*, 37, ventral. **aw** – antennomere width; **cl** – clypeal length; **cw** – clypeal width; **dbe** – distance between eyes; **el** – eye length; **ew** - eye width; **gl** – gular length; **gw** - gular width; **hl** - head length; **hw** – head width; **iw** – mandible internal width; **lig** – length of ligula; **ll** – length of labrum; **lw** - width of labrum; **men** – length of mentum; **ml** – mandibular length; **mol** – molar length; **mow** – molar width; **msl** – mediostipes length; **msw** - mediostipes width; **mtp** – medial tormal process length; **mw** – mandibular width; **pl** – pedicel length; **ptp** – posterior tormal process length; **sl** – scape length. Scale bar = 0.05 mm (Figs 32, 35); 0.1 mm (Figs 34, 36) and 0.5 mm (Figs 30 – 31, 33, 37).



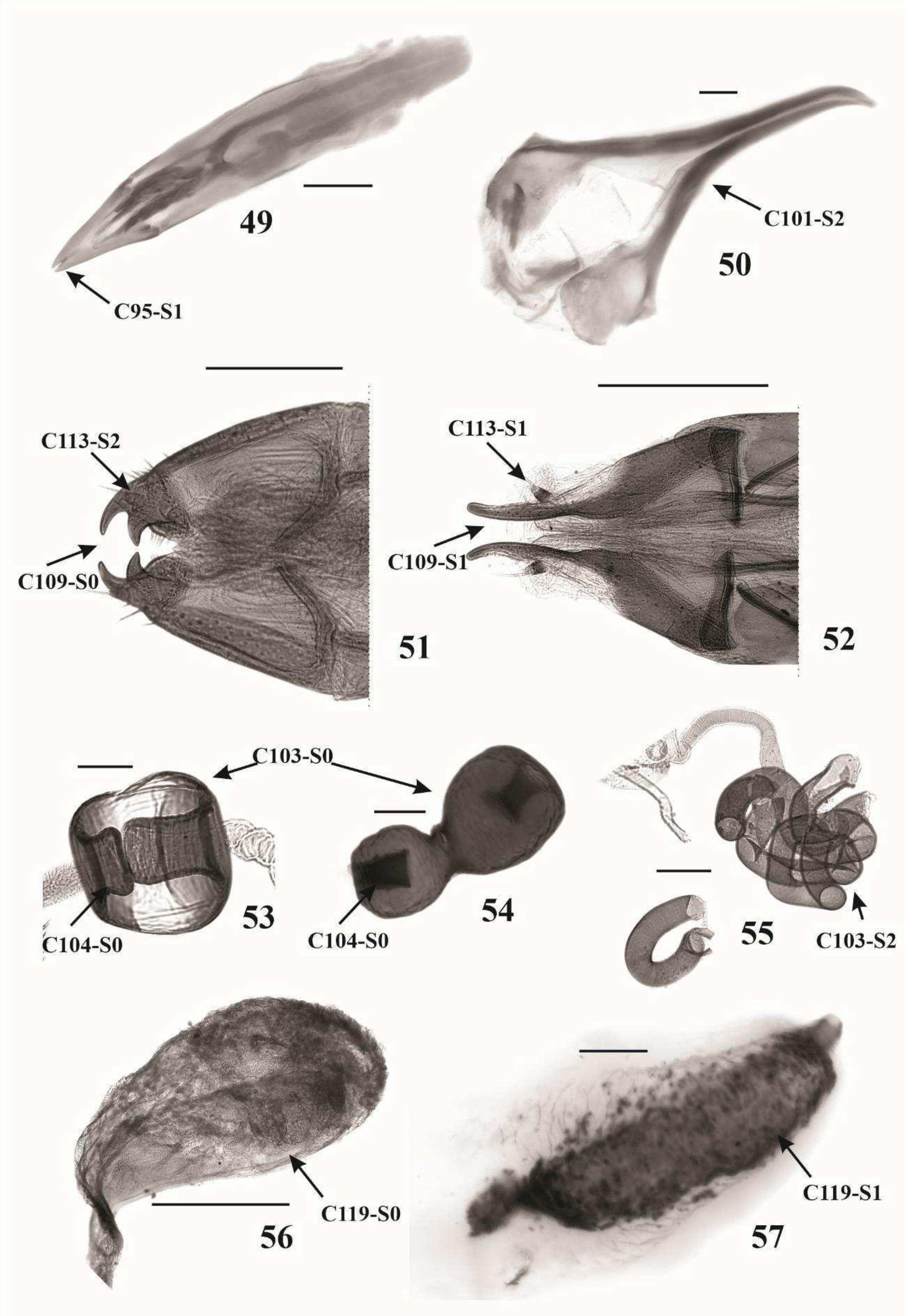
Figures 38 – 41. Prothorax, *Phaleria testacea*, 38, ventral; 39, frontal. Mesonotum, *Neomida luteonotata*, 40, dorsal. Metanotum, *Crypticus quisquillius*, 41, dorsal. **arm –** alar ridge of metascutelum; **asw –** antecostal suture width; **dc –** distance between procoxae; **mesl –** mesonotal length; **mesw -** mesonotal width; **metl –** metanotal length; **metw -** metanotal width; **msm –** mesoscutelum; **mso –** mesoscutum; **pap –** prosternal apophysis length; **pcw –** procoxal width; **pp –** prosternal process length; **prl –** prosternal length; **prw -** prosternal width; **ptl –** prothorax length; **ptw –** prothorax width; **sg –** scutellar groove. Scale bar = 0.05 mm (Fig. 41); 0.1 mm (Fig. 40) and 0.5 mm (Figs 38 – 39).



Figures 42 – 44. Meso and metaventrite, *Diaperis boleti*, 42, ventral. Metendosternite, *Myrmechixenus vaporariorum*, 43, dorsal. Hind wing, *Ceropria laticollis*, 44, dorsal. **af** – apical field; **hwl** – hind wing length; **la** – aperture angle of laminae; **lam** – metendosternite laminae length; **mcd** – distance between mesocoxae; **mcw** – mesocoxal width; **mf** – medial field; **mtd** – distance between metacoxae; **mtw** – metacoxal width; **mvl** – mesoventrite length; **mvtl** – metaventrite length; **mvtw** – metaventrite width; **mvw** – mesovantrite width; **stk** – metaventrite stalk length. Scale bar = 0.1 mm (Fig. 43); 0.5 mm (Fig. 42) and 1 mm (Fig. 44).



Figures 45 – 48. Elytrum, *Menimus ovalis*, 45, ventral. Proleg, *Phaleria testacea*, 46, left. Midleg, *Leiochrinus sauteri*, 47, right. Abdomen, *Scaphidema metallica*, 48, ventral. **abl –** abdominal length; **abw –** abdominal width; **els –** fragment of elytral suture; **llv –** larger length of ventrite 1; **pcl –** length of procoxa; **pfl –** length of profemur; **slv –** smaller length of ventrite 1. Scale bar = 0.05 mm (Fig. 45) and 0.1 mm (Figs 46 – 48).



Figures 49 – 57. Aedeagus, *Alphitophagus bifasciatus*, 49, ventral. Spiculum gastrale, *Leiochrinus sauteri*, 50, dorsal. Ovipositor, *Diaperis boleti*, 51, dorsal; *Phaleria testacea*, 52, dorsal. Spermatheca, *Diaperis boleti*, 53, dorsal; *Nilio (Linio) maculatus*, 54, dorsal; *Ectyche tuberculipennis*, 55, dorsal. Bursa copulatrix, *Neomida luteonotata*, 56, dorsal; *Nilio (Linio) maculatus*, 57, dorsal. Scale bar = 0.1 mm (Figs 49 – 50, 53 – 55, 57) and 0.5 mm (Figs 51 – 52, 56).

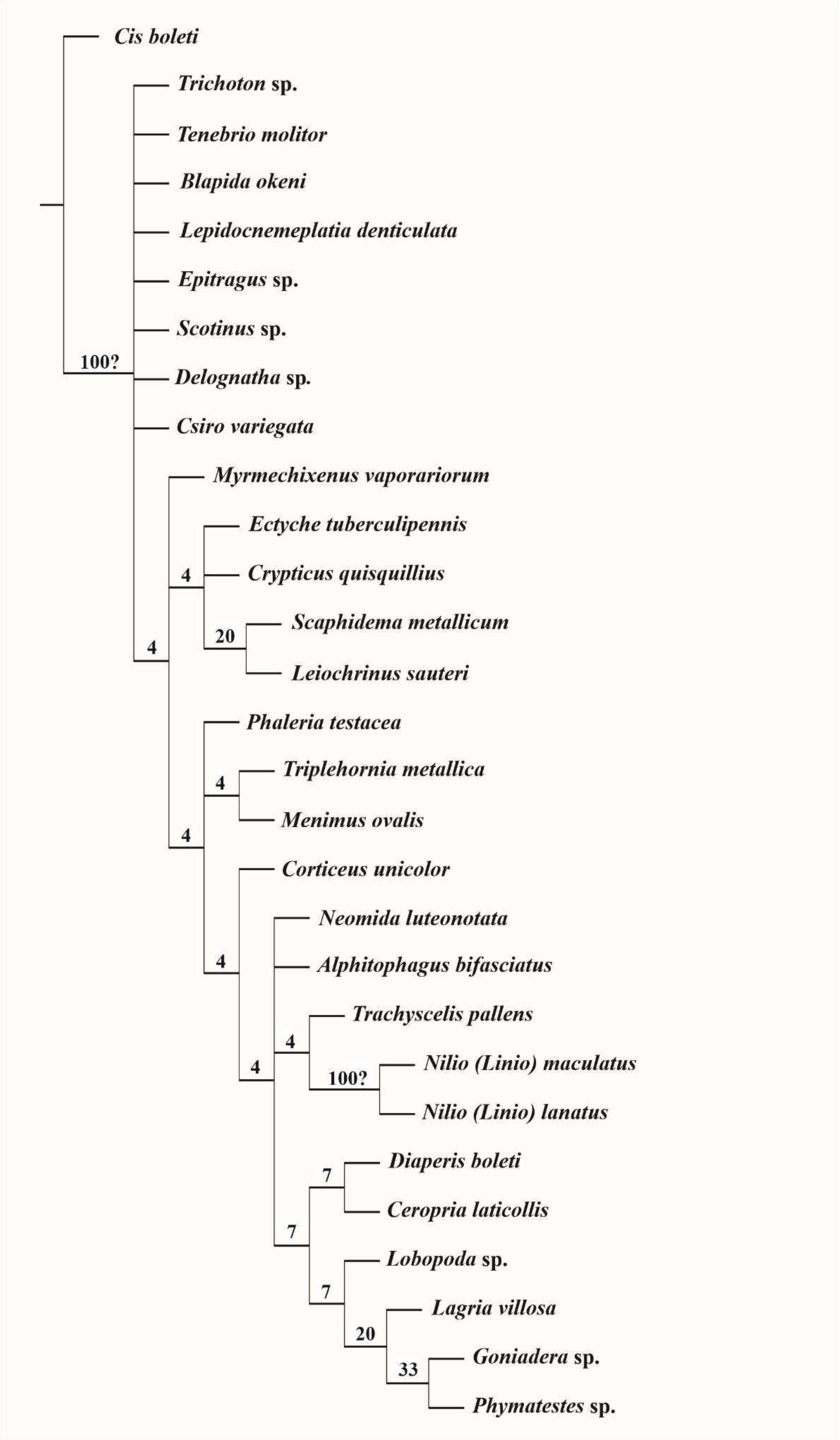


Figure 58. Strict consensus tree derived from the parsimony analysis with equal weights. Node values represent Bremer support. Unsupported clades are collapsed. Interrogation mark (?) represents the relative Bremer supports equal to absolute Bremer supports.

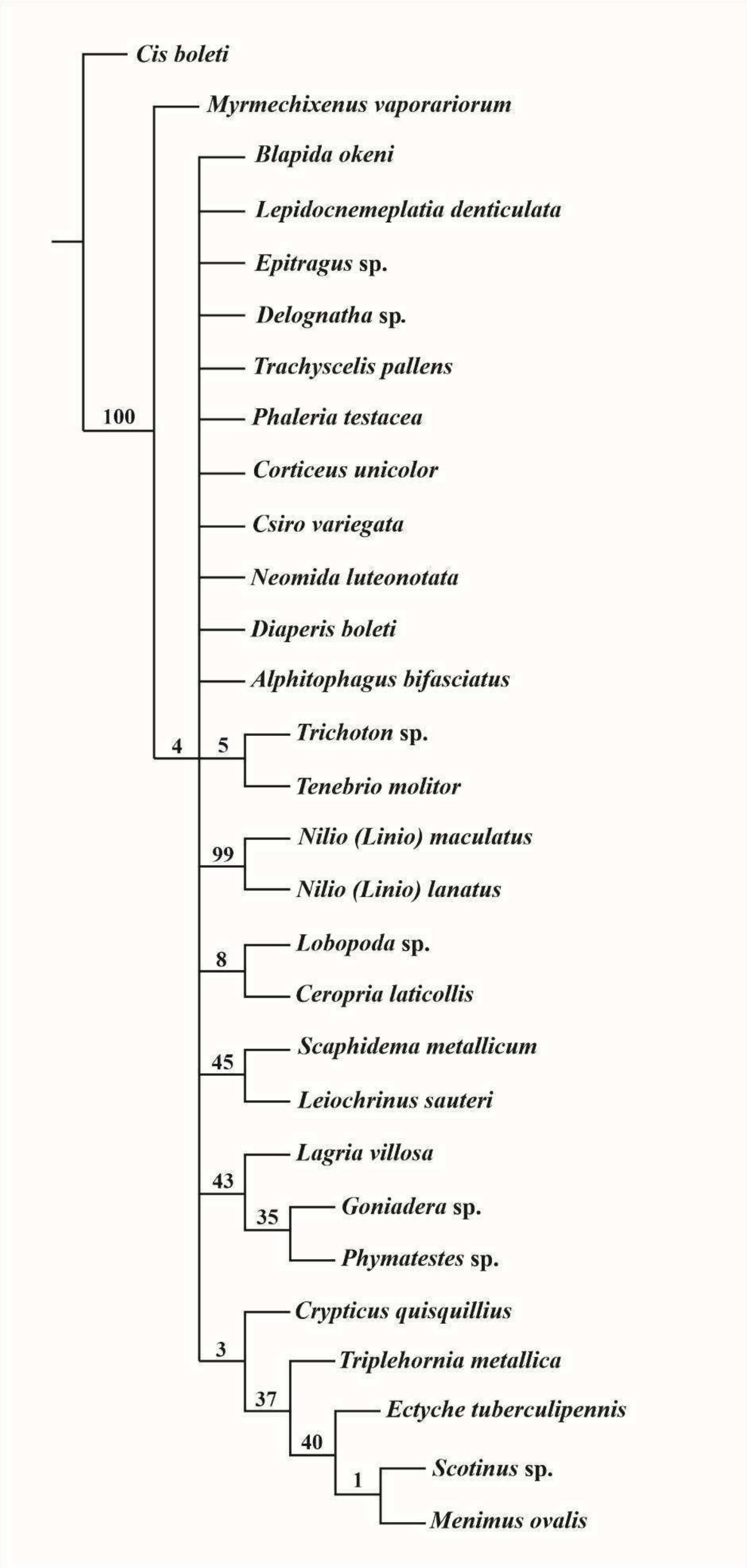


Figure 59. Strict consensus tree derived from the parsimony analysis with implied weights. Node values represent Symmetric Resampling support. Unsupported clades are collapsed.

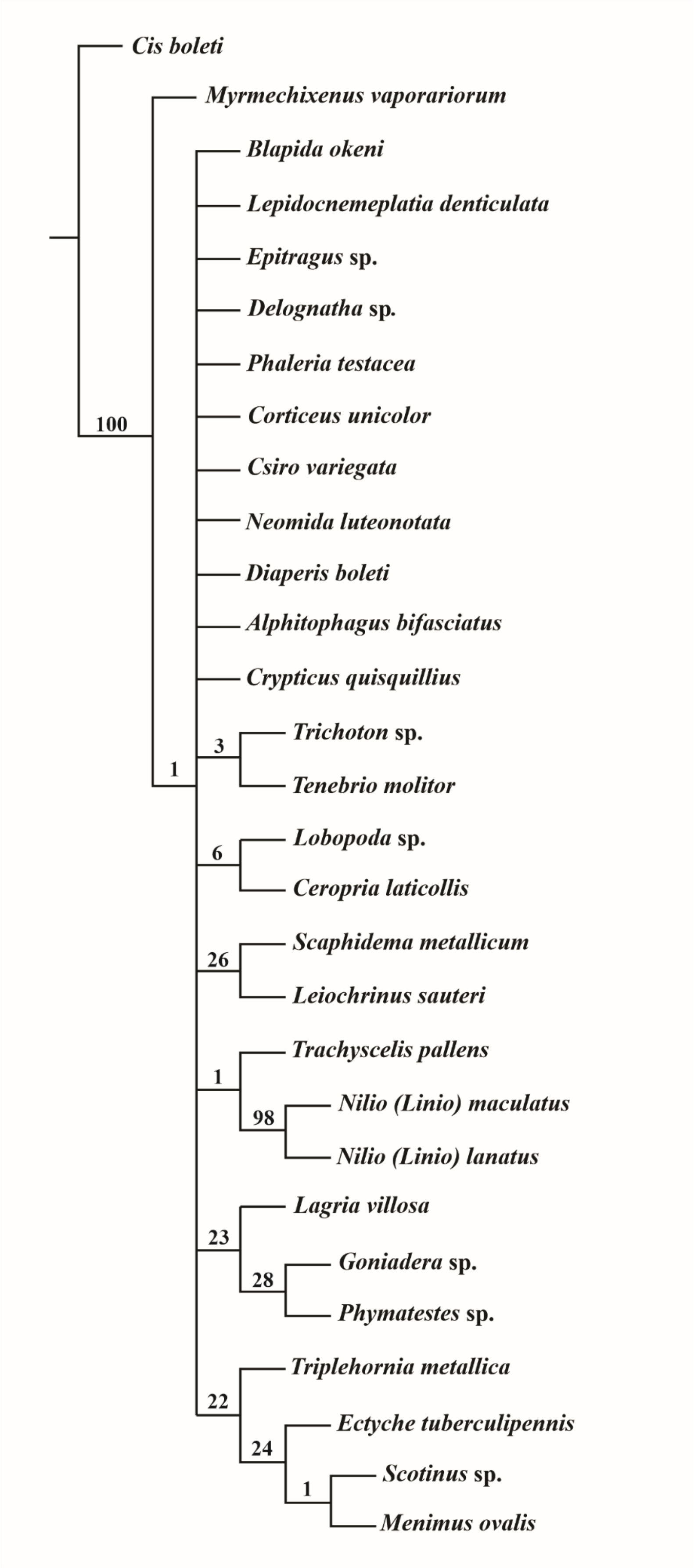


Figure 60. Strict consensus tree derived from the parsimony analysis with implied weights. Node values represent Bootstrap support. Unsupported clades are collapsed.

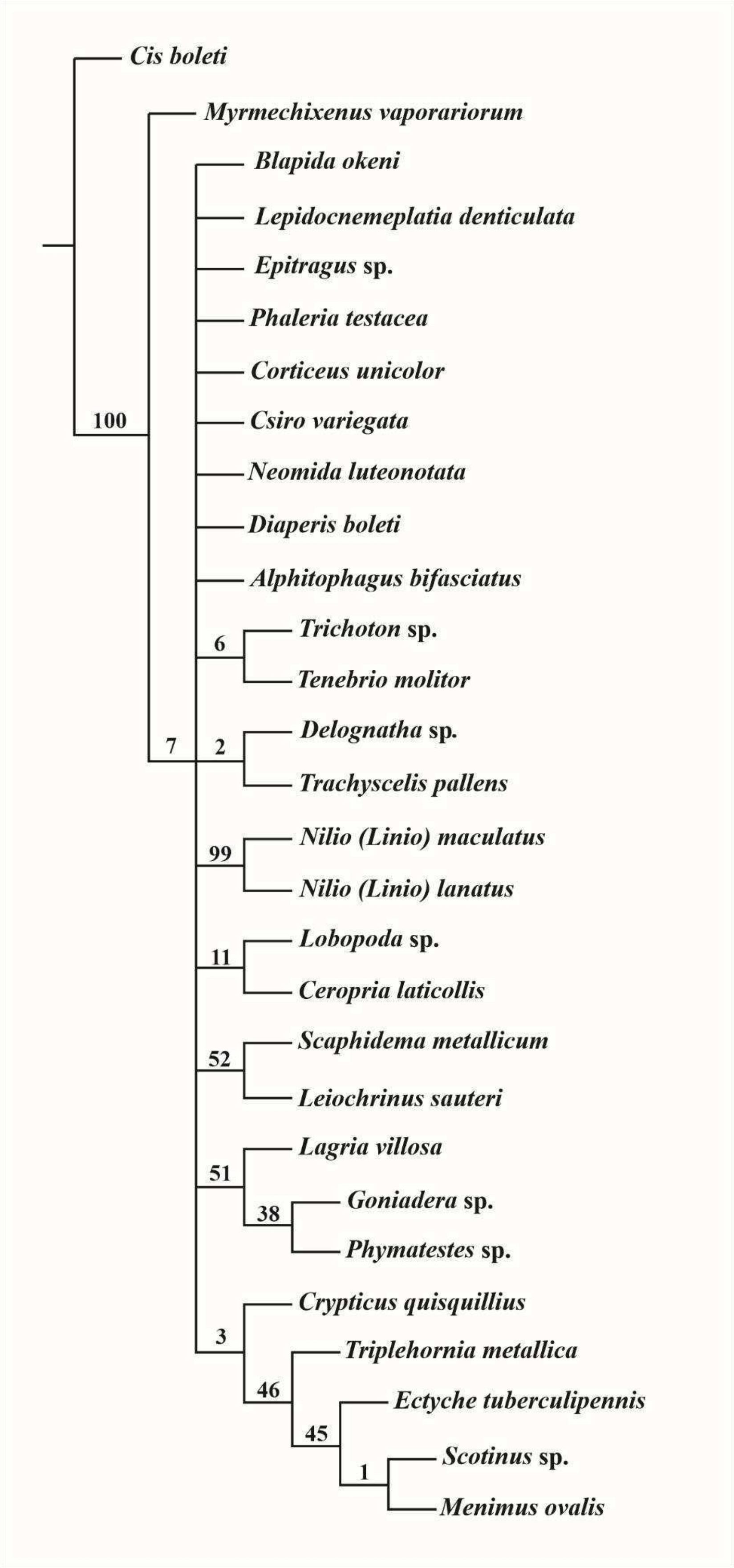


Figure 61. Strict consensus tree derived from the parsimony analysis with implied weights. Node values represent Jackknife support. Unsupported clades are collapsed.

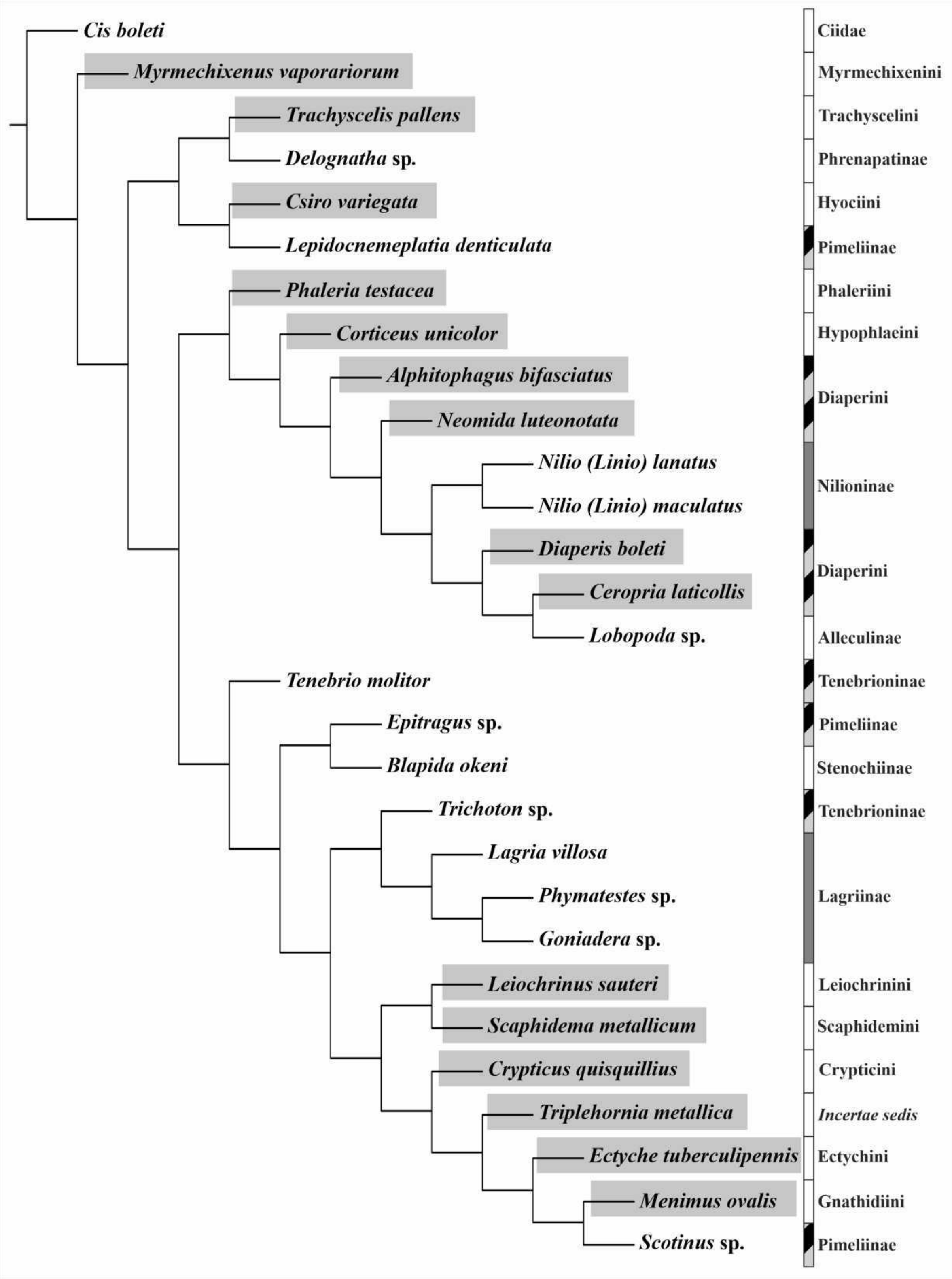


Figure 62. Phylogenetic tree for Diaperinae (Coleoptera: Tenebrionidae) recovered with IW analysis (k-value=6.106). Information of the suprageneric taxa is provided on the right of the figure. Taxa blocks colored with solid grey are monophyletic, blocks striped colored are non-monophyletic and white blocks represent taxa with no possible inference of monophyly. OTUs with light grey background correspond to Diaperinae taxa.

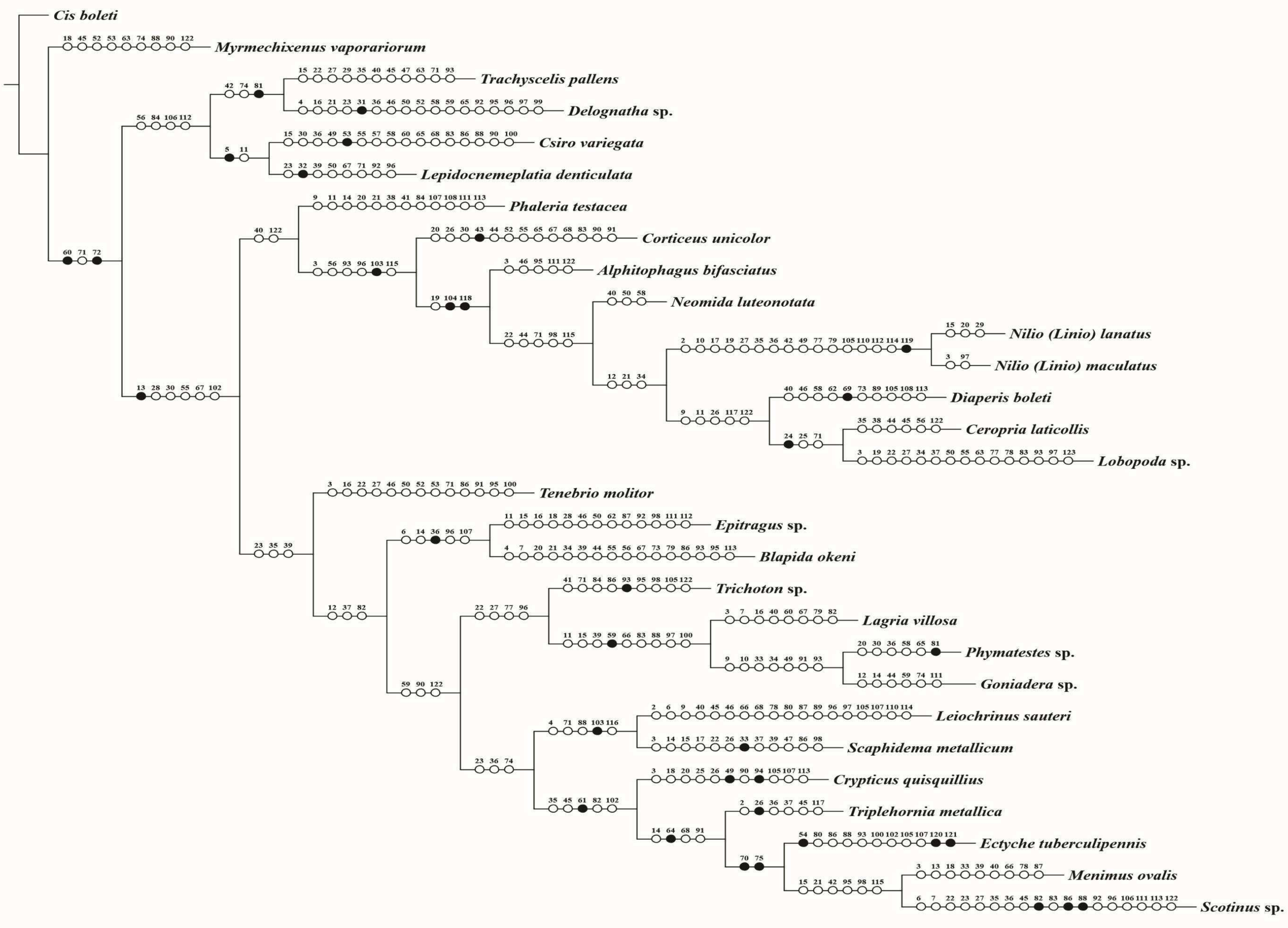


Figure 63. Phylogenetic tree for Diaperinae (Coleoptera: Tenebrionidae) showing the characters that support each clade. White dots represent homoplasy and black dots homology. Numbers above the dots represent the character number.

Table 1. Data matrix. Missing data are represented by a question mark (?) and inapplicable characters by a hyphen (-).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Crypticus quisquillius	0	0	0	0	1	0	1	0	1	1	0	0	0	1
Alphitophagus bifasciatus	0	0	0	0	1	0	1	0	1	0	0	1	0	1
Ceropria laticollis	0	0	1	0	1	0	1	0	0	0	1	0	0	1
Diaperis boleti	0	0	1	0	1	0	0	0	0	0	1	0	0	1
Neomida luteonotata	0	0	1	0	1	0	1	0	1	0	0	1	0	1
Ecthyche tuberculipennis	0	0	2	0	1	0	1	0	1	1	0	1	0	0
Menimus ovalis	0	0	1	0	1	0	1	0	1	1	0	0	1	-
Csiro variegata	0	0	2	0	0	0	1	0	1	1	1	1	1	-
Corticeus unicolor	0	0	1	0	1	0	1	0	1	0	0	1	0	1
Leiochrinus sauteri	0	1	2	1	-	1	0	0	0	1	0	0	0	1
Myrmechixenus vaporariorum	0	0	2	0	1	1	1	0	1	1	0	1	1	-
Phaleria testacea	0	0	2	0	1	0	1	0	0	0	1	1	0	0
Scaphidema metallicum	0	0	0	1	-	0	1	0	1	1	0	0	0	0
Trachyscelis pallens	0	0	1	0	1	1	1	0	1	1	0	1	1	-
Triplehornia metallica	0	1	?	?	?	0	1	0	1	1	?	1	0	0
Cis boleti	1	0	1	1	-	1	1	0	0	1	1	0	2	1
Lobopoda sp.	0	0	0	0	1	0	0	0	0	0	1	0	0	1
Lagria villosa	0	0	1	0	1	0	0	0	1	1	1	0	0	1
Phymatestes sp.	0	0	2	0	1	0	1	0	0	0	1	0	0	1
Goniadera sp.	0	0	2	0	1	0	1	0	0	0	1	1	0	0
Nilio (Linio) lanatus	0	1	1	0	1	0	1	0	1	1	0	0	0	1
Nilio (Linio) maculatus	0	1	0	0	1	0	1	0	1	1	0	0	0	1
Delognatha sp.	0	0	0	1	-	0	1	0	1	1	0	1	1	-
Scotinus sp.	0	0	2	0	1	1	1	0	1	1	0	0	0	0
Epitragus sp.	0	0	2	0	1	1	1	0	1	1	1	0	0	0
Lepidocnemeplatia denticulata	0	0	2	0	0	1	?	0	1	1	1	1	1	-
Blapida okeni	0	0	2	1	-	1	1	0	1	1	0	0	0	0
Tenebrio molitor	0	0	0	0	1	0	1	0	1	0	0	1	0	1
Trichoton sp.	0	0	2	0	1	0	1	0	1	1	0	0	0	1

Table 1. Data matrix. Missing data are represented by a question mark (?) and inapplicable characters by a hyphen (-). Continued.

15	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**
1	1	0	0	0	2	0	2	0	0	1	0	0	1	0	0	0	0	0
1	1	0	2	1	-	0	2	0	0	0	1	0	1	0	1	0	0	1
1	0	0	1	1	-	1	1	0	1	1	0	0	1	0	0	0	0	0
1	1	0	1	1	-	1	1	0	0	0	0	0	1	0	1	0	0	1
1	0	0	1	1	-	0	1	0	0	0	1	0	1	0	1	0	0	0
1	1	0	1	0	0	0	2	0	0	0	1	0	1	0	1	0	0	0
0	0	0	0	0	1	1	2	0	0	0	1	0	0	0	1	0	0	1
0	1	0	1	0	1	0	2	0	0	0	1	0	0	0	1	0	0	1
1	1	0	2	0	0	0	2	0	0	0	0	0	1	0	0	0	0	1
1	1	0	1	0	0	0	2	0	0	0	1	0	1	0	0	0	0	0
1	1	0	2	0	1	0	2	0	0	0	1	0	0	0	0	0	0	0
1	1	0	1	0	2	1	2	0	0	0	1	0	1	0	1	0	0	1
0	1	1	-	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2
0	1	1	-	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1
?	2	?	?	?	?	0	2	0	0	0	2	0	1	?	?	?	?	?
-	1	1	0	1	1	-	2	0	0	0	1	0	0	0	?	0	0	?
1	1	0	1	0	1	1	0	0	1	1	0	1	-	0	0	0	0	1
0	2	0	1	0	1	0	0	1	-	-	-	1	-	1	1	0	0	0
0	1	0	1	0	0	1	0	1	-	-	-	1	-	0	0	0	0	1
0	1	0	1	0	1	1	0	1	-	-	-	1	-	1	1	0	0	1
0	0	1	-	0	0	1	1	0	0	0	1	1	-	1	0	0	0	0
1	0	1	-	0	1	1	1	0	0	0	1	1	-	0	0	0	0	0
1	0	1	-	0	1	1	2	1	-	-	-	0	0	0	0	1	0	1
0	2	0	1	0	1	1	0	1	-	-	-	1	-	0	1	0	0	0
0	2	0	0	0	1	0	2	1	-	-	-	0	0	0	1	0	0	1
1	1	1	-	0	1	0	2	1	-	-	-	0	0	0	0	0	1	-
1	1	0	1	0	0	1	2	1	-	-	-	0	1	0	1	0	0	1
1	2	0	1	0	1	0	0	1	-	-	-	1	-	0	1	0	0	0
1	1	0	1	0	1	1	0	1	-	-	-	1	-	0	1	0	0	0

Table 1. Data matrix. Missing data are represented by a question mark (?) and inapplicable characters by a hyphen (-). Continued.

33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
0	0	2	1	0	0	0	1	1	1	1	0	1	0	0	2	0	0	0
1	0	1	0	0	1	1	1	1	1	1	1	2	0	0	1	0	0	0
0	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0
0	0	1	0	0	1	0	1	1	1	0	2	2	0	0	1	0	0	0
1	0	1	0	0	1	0	1	1	1	0	2	1	0	0	1	1	0	0
0	0	2	1	0	0	0	1	1	1	1	0	1	0	1	1	0	1	-
0	0	2	1	0	1	1	1	0	1	1	0	1	0	?	?	?	?	?
1	0	2	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0
1	0	1	0	0	1	1	1	0	0	2	0	1	0	0	1	0	0	1
0	1	2	1	0	0	1	1	1	1	1	2	2	0	0	1	0	0	0
0	0	1	0	0	1	0	1	1	1	1	0	1	0	0	1	0	0	1
0	0	1	0	1	1	1	0	0	1	1	0	1	0	0	1	0	0	0
0	1	2	0	0	1	0	1	1	1	1	1	1	1	0	1	0	0	0
1	1	1	0	0	1	1	1	0	1	1	2	1	1	0	1	0	0	0
?	?	1	0	?	?	?	1	?	1	1	2	?	?	?	?	?	?	?
1	?	1	0	1	1	1	1	1	1	2	1	1	0	0	0	1	0	0
1	0	1	1	0	1	1	1	1	1	0	2	1	0	0	1	1	0	0
0	1	1	1	0	1	1	1	1	1	1	2	1	1	0	1	0	0	0
1	1	2	1	0	1	0	1	1	1	1	0	1	1	0	0	0	0	0
1	1	1	1	0	1	0	1	1	1	2	0	1	0	0	0	0	0	0
0	1	2	0	0	1	1	1	0	1	0	2	1	0	0	0	0	0	0
0	1	2	0	0	1	1	1	0	1	0	2	1	0	0	0	0	0	0
0	0	2	0	0	1	0	1	0	1	1	1	0	0	0	1	2	0	1
0	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	1	1	-
0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	1	0	0
-	-	1	0	0	0	?	?	1	1	1	1	1	0	0	1	2	0	0
1	1	0	1	0	1	0	1	1	1	0	1	1	0	0	1	0	0	0
0	1	1	0	0	0	0	1	1	1	1	1	0	0	0	1	1	0	1
0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0

Table 1. Data matrix. Missing data are represented by a question mark (?) and inapplicable characters by a hyphen (-). Continued.

53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	1
1	0	0	1	?	?	?	?	0	1	?	0	1	0	1	0	1	0	1
1	0	0	0	0	1	1	1	0	1	0	0	1	0	2	0	1	0	1
1	0	0	1	1	0	1	1	0	0	0	0	1	1	2	0	0	0	2
1	0	0	1	0	0	1	1	0	1	0	0	1	1	1	0	1	0	2
1	1	-	-	?	?	?	?	2	1	0	1	-	0	0	1	-	1	-
?	?	?	?	?	?	?	?	1	0	0	1	-	1	0	1	-	1	-
0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	1	-	0	1
1	0	1	1	0	1	1	1	0	1	1	0	0	0	0	1	-	0	1
1	0	0	0	1	1	0	1	0	0	1	0	1	1	0	1	-	0	2
2	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	2
1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	1	0	1
1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	2
1	0	1	1	0	1	1	1	0	1	0	0	1	0	0	0	1	0	0
?	?	?	?	?	?	?	?	1	0	0	1	-	?	?	1	-	0	?
1	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	2
1	0	1	1	0	1	1	1	0	1	1	0	1	0	2	0	1	0	1
1	0	1	1	0	0	2	0	0	1	1	0	1	1	2	0	1	0	1
1	0	1	1	0	1	2	1	0	1	0	0	0	1	1	0	1	0	1
1	0	0	0	1	0	1	1	0	1	0	0	1	1	1	0	1	0	1
1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	0	1	0	2
1	0	0	1	1	1	1	1	0	1	0	0	1	1	0	0	1	0	2
1	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0	1
2	0	1	0	?	?	?	?	2	0	0	1	-	0	0	1	-	1	-
1	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1
1	0	1	1	0	1	1	1	0	1	1	0	1	0	1	0	1	0	2
1	0	1	1	0	1	1	1	0	1	1	0	1	0	0	0	1	0	1
2	0	0	0	0	1	1	1	0	1	1	0	1	0	1	0	1	0	2
1	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	1	0	0

Table 1. Data matrix. Missing data are represented by a question mark (?) and inapplicable characters by a hyphen (-). Continued.

72	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
0	1	1	0	0	1	1	0	1	1	0	1	1	1	0	0	0	1	0
0	1	0	0	0	1	1	0	1	1	0	1	1	1	0	0	0	1	0
0	1	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	1	0
0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0
0	1	1	0	0	1	1	0	1	1	0	1	1	1	0	0	0	1	0
-	-	-	1	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1
-	-	-	1	0	1	0	0	1	1	0	1	1	1	0	1	0	1	1
0	1	0	0	0	1	1	0	1	?	0	0	0	1	1	1	1	1	1
0	1	1	0	0	1	1	0	1	1	0	0	1	1	0	1	0	1	1
0	1	1	0	0	1	0	0	0	1	1	1	1	1	0	1	1	0	1
1	1	1	0	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1
0	1	0	0	0	1	1	0	1	1	0	1	0	1	0	1	0	1	0
0	1	1	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1
0	1	1	0	0	0	1	0	1	2	0	1	0	1	0	0	0	1	0
?	?	?	0	0	1	1	0	1	?	0	1	1	1	0	0	0	1	1
1	1	0	0	0	1	1	1	-	?	0	2	1	0	-	0	0	0	0
0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	0
0	1	0	0	0	0	0	1	-	1	0	0	1	1	0	0	1	1	1
0	1	0	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	1
0	1	1	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1
0	1	1	0	0	0	1	1	-	1	0	1	1	1	0	0	0	1	0
0	1	1	0	0	0	1	1	-	1	0	1	1	1	0	0	0	1	0
0	1	1	0	0	0	1	0	1	2	0	1	0	1	0	0	0	1	0
-		-	1	0	0	1	0	1	1	2	0	1	1	2	0	2	1	1
0	1	0	0	0	1	1	0	1	1	1	1	1	1	0	1	0	1	0
0	1	0	0	0	0	1	0	1	1	0	1	0	1	0	1	0	1	0
0	0	0	0	0	1	1	1	-	1	1	1	1	1	1	0	0	1	0
0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	0	0	1	0
0	1	0	0	0	0	1	0	1	1	1	1	0	1	1	0	0	1	1

Table 1. Data matrix. Missing data are represented by a question mark (?) and inapplicable characters by a hyphen (-). Continued.

91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109
0	0	0	1	-	1	0	0	0	0	2	1	-	-	1	0	1	1	-
0	0	1	0	1	0	0	1	?	?	?	0	0	0	2	0	0	1	-
0	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0	0	1	-
0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	1	-	0	0
0	0	1	0	0	0	0	0	0	0	2	0	0	0	2	0	0	1	-
1	0	1	0	0	1	1	0	0	1	-	0	2	1	0	0	1	1	-
1	0	0	0	1	1	1	1	0	0	2	1	-	-	2	0	0	1	-
0	0	0	0	0	1	1	1	0	1	-	1	-	-	0	1	-	1	-
1	0	1	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	-
0	0	0	0	0	0	1	0	0	0	2	0	1	1	0	0	2	1	-
0	0	0	0	0	1	1	1	0	0	2	?	?	?	1	0	1	1	-
0	0	0	0	0	1	1	1	0	0	2	0	2	1	2	0	2	0	1
0	0	0	0	0	1	0	1	0	0	2	0	1	1	2	0	0	1	-
0	0	1	0	0	1	1	0	0	0	1	1	-	-	0	1	-	1	-
1	0	?	?	?	?	?	?	?	?	?	1	-	-	2	0	0	1	-
1	0	0	0	1	2	1	0	1	0	0	1	-	-	1	0	1	1	-
0	0	0	0	0	0	1	0	0	0	1	?	?	?	2	0	0	1	-
0	0	0	0	0	0	1	0	0	1	-	0	2	1	2	0	0	1	-
1	0	1	0	0	0	1	0	0	1	-	?	?	?	2	0	0	1	-
1	0	1	0	0	0	1	0	0	1	-	?	?	?	2	0	0	1	-
0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	-	1	-
0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	-	1	-
0	1	0	0	1	0	0	0	1	-	-	?	?	?	?	?	?	?	?
1	1	0	0	1	2	1	1	0	0	2	?	?	?	2	1	-	1	-
0	1	0	0	0	2	0	1	0	0	2	?	?	?	2	0	1	1	-
0	1	0	0	0	2	1	1	0	0	2	?	?	?	?	?	?	?	?
0	0	1	0	1	2	0	0	0	0	2	?	?	?	2	0	1	1	-
1	0	0	0	1	1	0	0	0	1	-	?	?	?	1	0	0	1	-
0	0	2	0	1	0	0	1	0	0	2	?	?	?	1	0	0	1	-

Table 1. Data matrix. Missing data are represented by a question mark (?) and inapplicable characters by a hyphen (-). Continued.

110	111	112	113	114	115	116	117	118	119	120	121	122	123
0	0	0	1	0	0	0	1	1	-	1	1	0	1
0	1	0	0	0	1	0	1	0	0	1	1	1	1
0	0	0	0	0	2	0	0	0	0	1	1	1	1
0	0	0	2	0	2	0	0	0	0	1	1	2	1
0	0	0	0	0	2	0	1	0	0	1	1	0	1
0	0	0	0	0	0	0	1	1	-	0	0	0	1
0	0	0	0	0	2	1	-	-	-	1	1	0	1
0	0	1	-	0	0	0	1	1	-	1	1	2	0
0	0	0	0	0	1	0	1	1	-	1	1	0	1
1	-	0	0	1	-	1	-	-	-	1	1	0	1
0	1	0	0	0	0	?	?	?	?	?	1	0	1
0	1	0	1	0	0	?	?	?	?	1	1	0	1
0	0	0	0	0	1	1	-	-	-	1	1	0	1
0	0	1	-	0	1	0	1	1	-	1	1	1	1
0	0	0	0	0	0	0	0	1	-	1	1	0	1
1	-	0	0	0	2	?	?	?	?	?	?	2	1
0	0	0	0	0	2	?	?	?	?	?	1	2	0
0	0	0	0	0	0	0	1	1	-	1	1	0	1
0	0	0	0	?	?	0	1	1	-	?	1	0	1
0	1	0	0	0	1	?	?	?	?	?	1	0	1
1	-	1	-	1	-	0	1	0	1	?	1	0	1
1	-	1	-	1	-	0	1	0	1	?	1	0	1
?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	1	0	2	0	2	?	?	?	?	?	1	2	1
0	1	1	0	0	2	?	?	?	?	?	1	2	1
?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	0	2	0	2	?	?	?	?	?	1	2	1
0	0	0	0	0	2	0	1	1	-	?	1	2	1
0	0	0	0	0	2	0	1	1	-	?	1	1	1

APPENDIX I

In the label data, backslash indicates a new line in the same label and slash indicates a new label. Data within brackets indicates handwritten.

Outgroup

Tenebrionoidea: Ciidae

Cis boleti (Scopoli, 1763)

- One male and one female (CELC), labeled: "NEW ZEALAND: AK, Auckland City\ under Graftan Bridge\ on fungi on rotten wood\ 18.x.2010 S.E. Thorpe leg.".

Tenebrionidae: Alleculinae

Lobopoda sp. – Alleculini

- One male and one female (CELC), labeled: "BR: SP, Cerqueira César\ XXII.2000\ J. Carlos leg.".

Tenebrionidae: Lagriinae

Lagria villosa (Fabricius, 1781) – Lagriini

- One male (CELC), labeled: "BR: MG, Viçosa\ 02.v.2016\ P. Macedo leg.". One female (CELC): "BR: MG, Ipatinga\ Bom Retiro Centro\ i-vii.2017\ leg. J. Rocha Lucas". One female (CELC): "BR: MG, Viçosa\ Lourdes\ 22.xii.2019\ S. Aloquio & H.F. Aloquio leg.".

Phymatestes sp. – Goniaderini

- One male and one female (CELC), labeled: "BR: SP, Pederneiras\ Manual diurna\ 30.x.2015\ M. Bento leg.".

Goniadera sp. – Goniaderini

- Two males and one female (CELC), labeled: "BR: MG, Viçosa\ Ramos, Luz\ 4.i.2015\ C. Lopes-Andrade leg.".

Tenebrionidae: Nilioninae

Nilio (Linio) lanatus Germar, 1824

- One male and one female (CELC), labeled: “BR: RJ, Nova Friburgo\ Sans Souci, 18-20.i.2015\ 22,16ºS, 42,30ºO 1050m\ manual E.J. Grossi & C. Lopes-Andrade leg.”.

Nilio (Linio) maculatus Germar, 1824

- One male and one female (CELC), labeled: BR: MG, Viçosa\ Mata do Paraíso\ Manual noturna\ 28.vi.2016\ S. Aloquio & A. Orsetti leg.”.

Tenebrionidae: Phrenapatinae

Delognatha sp. – Phrenapatini

- One male and two females (CELC), labeled: “BR: MG, Viçosa\ ‘Mata da Biologia’\ 12.viii.2014\ Aloquio, Pecci-Maddalena, Orsetti & Lopes-Andrade leg.”.

Tenebrionidae: Pimeliinae

Epitragus sp. – Epitragini

- One male and one female (CELC), labeled: “BR: SP, Cerqueira César\ xii.2000\ J. Carlos leg.”.

Lepidocnemeplatia denticulata Triplehorn, 1987 – Cnemeplatini

- Two males and one female (CELC), labeled: “BR: MG, Rio Pardo de Minas\ ENT 01 23.ix.2019\ L.R. Santos & L.S. Fietto leg.”.

Scotinus sp. – Asidini

- One male and one female (CELC), labeled: “BR: SP, Santo André\ ReBio Alto da Serra de Piranapiacaba\ 750-890m 11.i.2007\ M. Uehara-Prado”.

Tenebrionidae: Stenochiinae

Blapida okeni Perty, 1830 – Cnodalonini

- One male (CELC), labeled: “BR: RJ, Nova Friburgo\ Sans Souci, 19-20.i.2015\ 22,16ºS, 42,30ºO, 1050m\ luz mista, E.J. Grossi & C. Lopes-Andrade leg.”. One female (CELC): “BR: PR, Mamborê\ 25.xii.2013\ S. Hosken leg.”.

Tenebrionidae: Tenebrioninae

Tenebrio molitor Linnaeus, 1758 – Tenebrionini

- One male and one female (CELC), labeled: “BR: MG, Viçosa\ xii.2019\ criação”.

Trichoton sp. – Opatrini

- One male and two females (CELC), labeled: “BR: MS, Corumbá\ RPPN Acurizal\ 17º50’13”S 57º33’31”W\ 24-26.vii.2012\ F.R. Tortato”.

Ingroup: Diaperinae

Crypticini

Crypticus quisquillius (Linnaeus, 1760)

- One male and one female (CELC), labeled: “Hu. C. Dömsöd\ Apajpuszta, 1953/ szikeslegelön\ fühálózva/ VII.10.\ leg Györffy\ & Zzirkó/ [quisquilium L.]\ det. Kaszab”. One female (CELC), labeled: “Kiskunsági N. P.\ Bugac, Nagybugac\ homokos rét.\ lótrágyából/ 1979.VII.26.\ leg. Migály/ [C. quisquilius\ (L.)]\ det. D. Skalóki, 19[81]”. One female (CELC), labeled: “Kiskunsági N. P.\ Fülöpháza\ homokbuckás\ egyelés/ 1977.VI.30. leg. Molnár/ [C. quisquilius\ (L.)]\ det. D. Szalóki, 19[81]”.

Diaperini: Diaperina

Diaperis boleti (Linnaeus, 1758)

- One male and one female (CELC), labeled: “Nadap\ Templom-hegy/ Nyírfa kéreg alól\ rostálva XI.13./ Hu. Occ. 1951\ Velencei-hegys\ legit\ Dr. Kaszab/ [boleti L.]\ det. Kaszab”. One male (CELC), labeled: “Orfalu\ 1983.V.26.\ Örség, Vas m.\ leg. Podlussány/ Diaperis\ boleti (L.)\ det. Szalóki, 1995.”.

Neomida luteonotata (Pic, 1926)

- Five males and one female (CELC), labeled: “BR: MG, Jequerí\ Ramos Novos\ 08.ix.2009\ E. Ferreira & E. Moura leg.”.

Alphitophagus bifasciatus (Say, 1823)

- One female (CELC), labeled: “IRAN: Mazandaran, Behshahr\ 27.vii.2010\ Abbas-Abad leg.”. Two males (CELC), labeled: “Hu. Pest. M.\ Szigetbecae\ 100m, [tehénistálló]/ rostálás\ 19[84.IX.9]\ leg. Merkl O./ *Alphitophagus*\ *bifasciatus*\ (Say, 1823)\ det. O. Merkl, 1994”.

Ceropria laticollis Fairmaire, 1903

- One male and two females (CELC), labeled: “LAOS: Ban Van Eua\ b. Vientiane\ II-III.1969\ leg. J. RONDON/ [laticollis Farm.]\ det. Kaszab”.

Ectychini

Ectyche tuberculipennis Bates, 1873

- One male and one female (ANIC), labeled: "West Australia\ Aug.-Sept.1926\ H. J. Carter/ [Ectyche\ tuberculipennis\ Bates]\ Id. By H. J. Carter".

Gnathidiini: Gnathidiina

Menimus ovalis (Allard, 1894)

- One male and two females (CELC), labeled: "India or. Shembagamur".

Hyociini: Hyociina

Csiro variegata (Blackburn, 1894)

- One female (CELC), labeled: "Australia, NW NSW.\ 102 km N from\ Broken Hill,\ Fowlers Gap/ at light\ 27-31.XII.1980\ leg. Hangay & Vojnits/ *Csiro variegata*\ (Blackburn, 1984)\ det. O. Merkl, 2016". Two males (CELC), labeled: "AUSTRALIA, N.T.\ Near Elsey Creek on Stuart\ Highway, (U. V. Ligth)\ S15º14'119" E133º06'749"/ *Hungarian Entomological*\ *Expedition in Australia*\ leg. G. Hangay, I. Rozner,\ A. Podlussány 3.XI.2000".

Hypophlaeini

Corticeus unicolor (Piller and Mitterpacher, 1783)

- One male (CELC), labeled: "Bükk-hegys.\ Nagyvisnyó/ Elzalak,\ 1956 VI.5-12/ Exc. Kaszab\ & Székessy/ [*Corticeus*\ *unicolor*\ PILL & MITT.]\ det. Szalóki 198[2].". One male and one female (CELC), labeled: "Kondorfa\ 1980.VIII.22./ Vas megye\ leg. Podlussány/ Corticeus\ unicolor\ Pill.\ et Mitt.\ det. Szalóki 1995."

Leiochrinini

Leiochrinus sauteri Kaszab, 1946

- One male and two females (CELC), labeled: "TAIWAN, Taipei Prov.\ Pi Hu, 450 m. 24º54'02"N\ 121º45'27"E, 4-5.IV.1997\ leg. L. Peregovits & A. Kun/ *Leiochrinus sauteri*\ Kaszab, 1946\ det. O Merkl, 1997".

Myrmechixenini

Myrmechixenus vaporariorum Guérin-Méneville, 1843

- One male and three females (CELC), labeled: “HUNG, Pest m.,\ Pusztazámor,\ autos hálózás este,\ 2006.VI.19., Merkl Ottó/ *Myrmechixenus\ vaporariorum* Guérin-Méneville, 1843\ det. O. Merkl, 2006.”

Phaleriini

Phaleria testacea Say, 1824

- Two males and one female (CELC), labeled: “BR: PE, Recife\ Praia do Pina\ 28.iii.2015\ P. Grossi leg.”.

Scaphidemini

Scaphidema metallica (Fabricius, 1792)

- One male and two females (CELC), labeled: “Kiskunsági N. P.\ Kunfehértó,\ Holdrutás erdó\ rostálás/ 1979.III.28.\ leg. Hármori./ [S. metallicum\ (Fabr.)]\ det. D. Szalóki, 19[81]”.

Trachyscelini

Trachyscelis pallens Champion, 1893

- One male and two females (CELC), labeled: “Sri Lanka\ Southern Province\ Galle Distrikt/ Habaraduwa\ 20.8.-4.9.1982\ H. J. Bremer leg./ *Trachyscelis pallens*\ Champion, 1893\ det. O. Merkl, 2005”.

Incertae sedis

Triplehornia metallica Matthews and Lawrence, 2005

- One female (ANIC), labeled: Bellenden Ker Range, NQ\ Cableway Base Stn. 100m\ 17 Oct- 9 Nov. 1981\ EARTHWATCH/QLD MUSEUM\ Pyrethrum knockdown/ Triplehornia\ metallica Matthews\ & Lawrence\ PARATYPE {blue label}”.

CONCLUSÕES GERAIS

Uma nova espécie de *Lelegeis* foi descrita para a Mata Atlântica brasileira e *Neanopidium mexicanum* foi redescrito, ambas espécies com descrição detalhada das terminálias abdominais de macho e fêmea. O estudo comparativo de terminálias abdominais de fêmeas de Diaperinae evidenciou diferenças importantes dentre as tribos, diferenças essas com possíveis sinais filogenéticos e de grande importância taxonômica, podendo ser utilizadas na delimitação de táxons.

A filogenia de Diaperinae baseada em caracteres morfológicos evidenciou a não monofilia da subfamília, corroborando com trabalhos previamente publicados, baseados em dados moleculares.

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